DUTCH ELM DISEASE

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FOREWORD

FOR MANY CENTURIES, the elm has been man's companion. No other tree has done more to improve man's environment by its majesty in the landscape and by taking the edge off the extremes of heat, glare, and wind. Over most of Europe and North America it was the one of the favored trees for streets, parks and gardens. Outside the towns, in a rural setting, the elm was widely planted around farmsteads, in lanes and along roads, in hedges and on field boundaries. Thus elm was often virtually the only tree used in such widely diverging habitats as midwestern towns in the United States, in the rolling British West Country, and in the windy coastal flatlands of Holland.

Elm was valued so highly partly for its products in terms of timber, shelter, shade, and beauty, but not less because of its low site requirements, including its remarkable ability to endure hardships like transplanting, soil compaction, a dry as well as a wet site, a continental climate as well as exposure to sea wind. This is generally combined with fast growth, so that a sizable tree can be established not too long after planting.

In our rapidly changing society, there is a change too in the uses we have for elm. Fifty years ago, elm timber was indispensable for building automobile bodies, and nobody can predict for what purpose elm will be utilized 50 years hence when the sapling planted now will be mature. Several of the old types of plantings that we now hate to lose are functionally outmoded and would not be replanted in the same way. But though uses may change, the unique combination of cultural properties and qualities of elm will be as rare and valuable in the future as they were in the past.

It would therefore be very shortsighted to allow the elm to lose its unique position in the landscape now that it is so severely threatened by Dutch elm disease. Instead we should make a big determined effort to save it for both the present and the future. Many of the remaining stately trees deserve to be protected both for their own merits and as links with a quieter past. New varieties are needed with resistance to the disease to be planted for the future. Research should help us to find and raise such varieties.

In the 53-year-old history of research on Dutch elm disease, the conference reported on in this publication marks a junction of several interests. First, it has been shown that the causal fungus contains both aggressive and relatively nonaggressive strains, and that an aggressive strain recently started a fresh epidemic of staggering proportions in Europe. Second, the long-expected breakthrough in chemical control of the disease by application of internally active fungicides seems to have been attained at least experimentally. Third, the biological control of the fungus-carrying beetles has entered a new phase with the identification of pheromones which play such an important role in their social life. These developments made an interdisciplinary meeting most timely.

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CHEMICAL CONTROL OF CERATOCYSTIS ULMI — AN OVERVIEW

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ONE OF THE EARLIEST documentations of the application of chemicals to trees is attributed to Leonardo da Vinci, who introduced liquid arsenical preparations into stems of fruit trees, by which he claimed to render the fruits toxic (*Anon. 1894*). From the Renaissance onward, occasional attempts were made to introduce into trees chemicals proposed to function physiologically or therapeutically.

These attempts were largely empirical in nature, and often shrouded in mystery. Campana (*1970*) stated that, "In modern times, the magic has been replaced by chemical logic, but unfortunately, some of the mystery and chicanery persist in false claims for cures not supported by experimental evidence."

Not until the twentieth century did there emerge a real interest in fungitoxicology and chemotherapy accompanied by sound scientific investigation; the art preceded the science. Significant accomplishments on the possible use of fungitoxicants in the control of vascular disease in woody plants have been recorded in the literature only within the last decade. Notable and rather extensive research on the chemical control of *Fusarium oxysporum* and *Ceratocystis ulmi*

had been reported from the Connecticut Agricultural Experiment Station beginning in the early 1940s; these efforts have been summarized by Zentmyer *et al.* (*1946*). Various problems and needs attendant to the systemic chemical control of these diseases have previously been reviewed (*Campana 1970, Dimond 1968, Erwin 1973, Stipes 1971*).

The chemical management of Dutch elm disease (DED) is a triparitite consideration in which the compounds have been used (1) to prevent transmission of the pathogen by its insect vectors, (2) to retard local spread of the fungus through root grafts, and (3) to control the pathogen directly or indirectly. The earliest chemicals used in the practical management of the disease were insecticides. The earliest and most effective of these was DDT (dichlorodiphenyltrichloroethane) (*Whitten and Swingle 1964*) but its use has been lost recently as a result of severe restrictive action by the United States Environmental Protection Agency (*Hays 1969*). In the early 1960s, the insecticide Bidrin (3-[dimethoxyphosphenyl-oxy]-N, N-dimethyl-cis-crotonamide), administered by Mauget capsules (J. J. Mauget Company, Burbank, California), was used with some degree of success. However, because of the narrow margin between phytotoxicity and control, Lincoln (*1967*) suggested that its further use was impractical, although his conclusions have not been totally accepted.

In addition to insecticides, Neely and Himelick (*1965*) and Smalley (*1965*) reported the effectiveness of the soil sterilant Vapam (sodium methyldithiocarbamate) as a chemical root-pruning compound for preventing root-graft transmission of the pathogen between contiguous healthy and diseased trees. Most laboratories and disease-control advisory agencies in the United States now strongly urge the careful use of this chemical.

The main theme of this section of our meeting concerns the third consideration, the chemical management of disease control with fungitoxicants.

Many compounds have been employed in attempts to control DED since the disease was discovered in Europe in 1919 (*Schwarz 1922*) and in the United States in 1930 (*May 1930*). One unpublished list cites 459 chemicals tested, and without question this is a minimum number. Occasional published and unpublished reports on these compounds appeared prior to the advent of the "benzimidazole era" in 1967. The discovery of benzimidazole and related fungitoxicants (*Delp and Klopping 1968, Ishii 1971, Staron et al. 1966, Weinke et al. 1969*), which exhibit both systemicity in elm and varying levels of activity against *C. ulmi*, have been under intensive evaluation recently.

Benomyl and its hydrolytic product, methyl 2-benzimidazolecarbamate (MBC) (*Clemons and Sisler 1969, Sims et al. 1969*) seem to be especially active against the pathogen and effective in controlling DED under specific experimental situations. At this point, I wish to emphasize that the "solubilized benomyl" alluded to both in current discussions and in the literature on the chemotherapy of DED is a misnomer, at least in part; it is probably solubilized MBC that was prepared from benomyl treated generally with a regimen of acetone, heat, and one of the mineral acids (*Kondo et al. 1973, McWain and Gregory 1973, Smalley et al. 1973*).

One of the several desirable attributes of benomyl and MBC is the safety margin between the *dosis tolerata* and the *dosis curativa* that constitute Ehrlich's chemotherapeutic index. As the gap between these *doses* shortens (as they approach identity), then the candidate compound becomes less suitable. A wide margin of safety between these *doses* is required in cases where dosage standardization is difficult or nearly impossible to achieve and because of lack of precision in practical control efforts or errors made by applicators.

Thiophanate methyl (*Ishii 1971*), which has an antifungal spectrum similar to that of benomyl, is likewise transformed to MBC (*Selling et al. 1970*). Ceratocide, a recent invention

of Lowden, Inc., Needham Heights, Massachusetts, which contains nystatin, is also under current appraisal (*A.C. Costonis 1973*, personal communication). Other compounds have been used with varying levels of success, while some are undergoing or awaiting evaluation. One foreboding attribute of some of these systemic fungitoxicants in the control of vascular as well as other diseases is their peculiar ability to induce tolerance within populations of the target organism (*Kirby 1972*).

Benomyl, MBC, and other compounds employed in the control of DED are referred to as *fungicides*, which means literally that they *kill* the causal fungus. Certain evidence has accumulated that indicates that they are functioning as *fungistats*: they would simply inhibit vegetative growth, germination or sporulation of the pathogen while in the presence of the compound. Therefore, until this question has been answered, it is suggested that we refer to these compounds as *fungitoxicants*, a term that would accurately include either phenomenon.

Very early surgical removal of symptomatic branches has resulted in significant disease control in trees naturally infected in the crown (*Marsden 1952*). Although undocumented conclusively in the literature at this time, certain investigators have indicated that early surgery, as an adjunct to the administration of fungitoxicants, has further increased the survival rate of diseased trees.

APPLICATION METHODOLOGY

The choice of attack in administering the candidate compound so that the desired response can be effected is a dichotomous scheme that becomes more complex as one progresses. First, because the elm tree is composed of roots, stems, and leaves, these are obviously the only three sites from which to choose for chemical administration. Second, we know that, of all tissues, the recently-formed xylem constitutes the in-

fection court and is the tissue in which the spreading vascular lesion develops. Therefore the chemoprophylactant (preventive or protective agent) or chemotherapeutant (curative agent) must reach this tissue at the *right time* and at the *proper concentration* and *duration* to be effective. At this point, then, judging by these and other considerations, one must choose the most proficient method involving a topical (plant surface) or systemic (internal) approach by which to satisfy as many requisites as possible for disease control. In short, we are ultimately striving for efficacy, economy, general long-term acceptability, and legality, all in one package.

Each technique poses virtues as well as weaknesses, and one method may be applicable to one landscape situation, but not to another. Each technique, therefore, merits evaluation. The input and contribution provided by the conferees present here may help to establish better guidelines to individual and corporate research efforts.

I have attempted to provide a summation and overview of relatively recent published work by highlighting different approaches being employed in disease control by various laboratories, while trying to avoid complete literature citations and minutia in experimental designs; these will be appropriately given as desired by the various discussants. Table 1 annotates some strengths and weaknesses of various methods. The list is by no means exhaustive, and the ratings are subject to a difference of opinion based upon variations in experience or knowledge, either present or not extant in the literature available to date.

Foliar Administration

Spray applications of benomyl or MBC to the crown area of elm trees have been viewed usually as a preventive method. Here there are two goals: the coverage of twig crotches (a major infection court of the disease), and the uptake by and translocation of the fungitoxicant within treated leaves and

Table 1.—An evaluation of methods of chemical administration for control of Dutch elm disease[1]

Methodology feature	Tissue treated and method used						
			Root		Stem (bole)		
	Leaves (spray)	Bark (topical appl.)	Soil inj.	Root inj.	GFR[2]	TID[3]	Pressure inj.
1. No stem wounding	+	+	+	+	0	0	0
2. No root wounding	+	+	+?	0	+	+	+
3. Accessible treatment area	+	+	+?	+?	+	+	+
4. General skill required	+	+	+	0?	+?	+	+?
5. Annual treatments not required (long-term protection)	0	+?	+	0?	0	0	0
6. Effective uptake	0?	+?	+	+	+	+?	+
7. Uniform distribution	+	+?	+	+	+?	+?	+?
8. Small dosages required	+?	+	0?	+	+?	+	+?
9. Prophylactic (preventive)	+	+	+	+	+	+	+
10. Therapeutic (curative)	0	0?	0?	+?	+?	+?	+?
11. Aerial environment not contaminated	0	+	+	+	+	+	+
12. Soil not contaminated	+	+	0	+	+	+	+
13. Relatively economical (labor/materials)	+	+	0?	0	+	+	+?
14. Low vandalism potential	+	0?	+	+	0	+	+
15. Low disease transmission risk	+	+	+	+	0	0	0
16. Demonstrated efficacy in disease control	+	+?	+	+?	+?	+?	+
17. EPA[4] registered	+	0	0	0	+[5]	0	0

[1] + = item description generally true.
0 = item description generally false.
[2] Gravity-feed reservoir.
[3] Trunk-implantation device.
[4] Environmental Protection Agency, U.S. Government.
[5] Mauget reservoir only.

stems. The possibility of therapeutic activity, although remote, has been envisioned.

Although spray treatments would require conventional equipment now used in insecticide applications, and are endowed with many desirable features (table 1), there remains the objectionable feature of aerial contamination and the various meteorological and environmental problems attendant to these operations. Due to the low mammalian toxicity levels of benomyl (*Anon. 1967*), these objectives may be accorded a role of minor concern.

Hart (*1972*) and Smalley *et al.* (*1973*) reported significant disease control in new natural infections following mistblower spray applications; both also reported, under specific situations, the presence of a fungitoxicant in xylem tissues in the treated zone. Smalley provided evidence that benomyl or its derivative, MBC, may have entered through lenticels rather than through intact bark or leaves. Upham and Delp (*1973*) recently indicated that twentyfold more benomyl than MBC entered and moved within herbaceous plant leaves, but that movement was confined to the transpiration stream. Numerous factors such as additives (*Stipes and Oderwald, 1970*) and possibly others (atmospheric humidity, formulation procedures, concentration, etc.) could be important variables in explaining disparities in results. Generally, foliar application appears to be a promising approach to pursue, based on these results and on those of Buchenauer and Erwin (*1971*), who demonstrated both preventive and curative effects of Verticillium wilt of cotton, using foliar sprays of benomyl and thiabendazole.

Bark Administration

Application of protective or therapeutic agents to the bark has several attractive features. Mechanical wounding is avoided and the treatment area is unlimited. If permeation by the candidate compound is effected, the outermost active xylem is reached first, with attendant acropetal (upward)

uptake. Little if any environmental contamination results, and sustained uptake with uniform distribution and protection should be possible along with other beneficial effects. On the debit side of the ledger, bark is often difficult to permeate because of its chemical and physical composition, and especially because of thickness in older trees. Treatment also might be injurious to phloem and cambium tissues, especially if compounds were applied in high concentrations.

Among earlier attempts at bark treatment were those of Beckman (*1959*) and Smalley (*1962*) who administered chlorinated organic acid derivatives to induce morphological reisstance. The *dosis tolerata* and *dosis curativa* were so nearly equal that further testing was stopped. Stipes and Schreiber (*1966*) observed significant disease control with certain fungitoxicants and antifungal antibiotics administered to the bark prior to artificial inoculation. The test was repeated the following year with less encouraging results. In possibly the earliest report of the control of DED with benomyl (*Stipes 1969*), solutions of benomyl in dimethyl sulfoxide (DMSO) applied to small branches prior to artificial inoculation greatly suppressed foliar symptoms. This method might be adaptable to trunk application, although it was not tried because of bark thickness on trees available for treatment.

If permeation of the bark is achieved, more information must be gleaned on means of translocating compounds through it, undegraded and unabsorbed, to the sapwood, where it can be mobilized within the transpiration stream to the infection court of natural *Scolytus*- induced infections in the tree crowns.

Stem (Bole) Administration

The greatest current flurry of activity in the chemical management of DED is in the application of benomyl and MBC to the sapwood of the trunk. This is being achieved by gravity feed and pressure-injection methods. (pressurized

delivery systems). For the sake of etymological accuracy and to avoid confusion, I suggest that we refer to *injection* only as the *forceful introduction* of chemicals into trees by pressurized apparatuses. Perhaps the *gravity-feed reservoir* (GFR) might best describe the technique by which fluids, contained in reservoirs outside the tree, are administered or applied *via* tubes connected to insertion holes drilled or forced into the sapwood. Uptake is hereby achieved by gravity and transpirational forces. Various versions of the GFR system were developed many years ago (*May 1941*). The J.J. Mauget Company (Burbank, California) markets low-volume plastic GFR and pressure (8-10 psi) injection units, the former being licensed in 1972 by the Environmental Protection Agency (Supplemental label Reg. No. 352-354) for use in the control of DED with Benlate (*Anon. 1972, Heffernan 1968*). Two other low-volume *truck-implantation devices* (TIDs) have been developed in which uptake is designed to occur, primarily by transpirational forces within the young sapwood: the SIReservoir system (Systemic Implant Reservoir Corp., Madison, Wisconsin) and Medicaps (Creative Sales, Inc., Fremont, Nebraska). These units, filled with a benomyl formulation, are implanted within pre-drilled holes in the sapwood after which release and uptake are supposed to occur.

Various advantages and disadvantages of pressurized stem injection are listed in table 1. In addition, since dilution of a chemical within the treated sapstream applied by other methods can be a critical factor as to whether the chemical is efficacious, large volumes are required to protect the vascular tissues. In an effort to preclude phytotoxicity of concentrated formulations at the point of entry, larger volumes of a lower chemical concentration can be administered uniformly to large trees within minutes by this system. Also, uptake of suspensions is more rapid and complete by pressure injection than by the GFR method.

Pressurized delivery systems or injection units have been

developed recently by the USDA Forest Service, Delaware, Ohio (*Jones and Gregory 1971*), USDA Agricultural Research Service, Delaware, Ohio (*Hock and Wilson 1972*), Illinois Natural History Survey, Urbana (*Himelick 1972*), Elm Research Institute, Harrisville, N.H. (*J.P. Hansel 1972, personal communication*), and the United Kingdom Forestry Commission, Farnham, Surrey, England (*J.N.Gibbs 1972, personal communication*). These are basically similar in design.

Because of the very recent development of high-pressure injection units and the recent testing of certain GFR and related devices, few results on efficacy in disease control are available. However, certain trends are emerging. Smalley (*1973*) and Gregory *et al.* (*1973*) observed preventive and curative responses in DED, using stem-administered benomyl. Both laboratories reported that therapy was successful only if initiated in very early stages. Jones *et al.* (*1973*) effected preventive and curative responses in oak wilt, but likewise indicated that early therapy was essential. In GFR and injection studies, most investigators have emphasized greater efficacy with "solubilized benomyl" over wettable powder suspensions as currently registered by the Environmental Protection Agency (*Anon. 1972*).

Root Administration and Soil Treatment

The rhizosphere and root system itself are propitious sites for applying disease-control compounds. Since sap movement is upward, once the compound gains access to the xylem, it can be transported uniformly throughout the vascular system. Although certain objectionable features must be acknowledged, this method has strong positive features, as borne out by recent findings in disease control.

One of these virtues, in soil treatment, is the sustained dosage that allows continuous uptake of the fungitoxicant, not realized with single-shot stem injections; this long-term

dosage system could well be more essential for disease control than is presently thought. For example, in the chemotherapy of Streptococcus infections in animals, a certain level of penicillin or other suitable antibiotic is administered initially; a high titer is then maintained by repeated doses over a period of days to inhibit cell wall systhesis in newly-dividing cells (*Salton 1960*) and to allow the phagocytes in the bloodstream to destroy mature cells. Since elm trees have neither a circulatory system by which to continuously recycle the therapeutant nor phagocytes to destroy the fungal pathogen, sustained protection or therapy would appear desirable, if not essential. Further, it is not likely that the therapeutant is able to permeate infected tissues and protect during the susceptible period the uninvaded xylem with one or two stem injections.

The assay of benomyl against DED was begun with soil applications (*Biehn and Dimond 1970, Hock et al. 1970, Smalley 1971, Stipes 1969*). Hydrogen ion concentration also has been shown to be a limiting factor in dissolution, absorption, distribution, and accumulation (*Prasad 1972*). Success (*Smalley et al. 1973*), as well as failure (*Stipes 1972*), has been reported in suppressing symptoms in established infection by therapeutic soil injections. As with other methods, however, preventive soil injections of benomyl have proved to be very effective (*Smalley 1971, Stipes 1973*). It should be emphasized that minimum dosage levels for effective disease control by soil injection have not yet been determined. This should obviate the current criticisms of excessive dosages being required for successful preventive or curative management of disease. An acceptable dose could probably be determined whereby efficacy and residue requirements could be satisfied. Although benomyl is degraded in soil, it has been reported to persist there for at least 27 months after application (*Biehn 1973*). This may prove to be a weakness as well as a strength, should attempts be made for its registration for public use.

Kondo (*1972*) and Kondo and Huntley (*1973*) have revealed a new and interesting injection method of introducing dyes and MBC-phosphate at the ends of severed buttress roots; uniform distribution, a desirable feature in systemic protection or therapy, was achieved. In treating symptomatic trees, they emphasized the correlation of maximum disease arrest and treatment initiation at early symptom development. Kondo *et al.* (*1973*) reported that various salts of MBC were more fungitoxic to the pathogen and less phytotoxic to the host.

SUMMARY COMMENTS AND PROGNOSTICATION

1. Various chemical application techniques for the control of DED, each with merits and weaknesses and suited for unique landscape situations, have been developed and are being evaluated at different levels of activity in laboratories in Canada, England, and the United States. Stem injections and GFR (gravity-feed reservoir) systems, in addition to soil or root application techniques, have received the broadest attention to date.
2. Chemical formulation and solubilization problems with benomyl and other candidate compounds have been accorded prime consideration, so that rapid uptake, uniform distribution, and attendant disease control might be achieved.
3. Noteworthy success has been reported in the treatment as well as prevention of DED with benomyl, although the latter is the signally superior approach. Recurrent, root graft-transmitted and advanced infections have not been viewed as promising candidates for successful treatments, although they should not be considered hopeless at this time.
4. Success in attempts at therapy in new crown infections has appeared to be enhanced by the combination with

prompt surgical removal of symptomatic branches that serve as large reservoirs of inoculum.

5. The chemical management of DED with the aid of fungitoxicants must be considered as a supplement to, and not a substitute for, integrated control consisting of insect vector control with insecticides and sanitation, early surgical removal of symptomatic branches (new crown infections), together with the prevention of root graft transmission.
6. The possible development of tolerance to systemic fungitoxicants in current wild populations of *C. ulmi* would appear to be a rule and not an exception (*Kirby 1972*). Therefore, consideration of this phenomenon should be included in future research and disease-control activities.
7. The outlook for control of DED has never been brighter nor the research arena ever more challenging and exciting. But at the successful end of our ventures, the ledger sheet must reveal in the credit column a system that is characterized by acceptable efficacy, minimal injury to the tree, federal and state governmental approval, and economic as well as application feasibility.

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DISCUSSION

Chairman: E. B. Smalley, University of Wisconsin,
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The chairman opened the discussion by presenting some of the results of his own 1971-73 tests on control of DED with benomyl, with slides showing various techniques of application. His abstracted conclusions indicated that remission of naturally or artificially induced Dutch elm disease in its early stages was achieved in a high percentage of elms treated by trunk or soil injection with benomyl, methyl 1-(butylcarbamoyl)-2 benzimidazolecarbamate. Early, fast-developing infections, such as occur with root-graft transmissions or recurrent disease, were not controlled by such treatments except where treatment was combined with removal of the infected branches. Mass protection was achieved in municipal situations by spring application of benomyl either by trunk injection or by mist-blown foliar sprays. In such treatments, the incidence of new infection in untreated trees was 3 to 4 times greater than in the treated trees. Analysis and bioassay of greenhouse elms sprayed with benomyl formulations suggested that systemic uptake of benomyl was accomplished in small branches through the lenticels. Improved solubilization of the benomyl without phytotoxicity, as indicated by both *in vitro* and *in vivo* tests, was achieved using acetone-HC1 solutions and in suspension with Tween 80, polyoxyethylene sorbitan monoleate, and Tergitol NPX, polyglycol ethers. Lactic acid solubilization yielded impressive activity, but solutions were extremely phytotoxic at all dilutions tested.

Prasad: Uptake of MBC by the leaves is poor, as was shown in experiments with MBC marked with C^{14}. Uptake by the roots is far more efficient.

Chairman: Foliar sprays seem to be relatively ineffective, probably partly because of insufficient wetting of the twigs. Lenticels seem to take up the material rather well.

Van Alfen: Is registration of MBC for trunk injection of elm trees to be expected? I am under the impression that MBC will not be marketed in the United States. Is this correct? We found that a suspension of the 50 WP formulation of benomyl pressure injected into the trunks of large elm trees was no more effective than a Methoxychlor spray schedule in preventing Dutch elm disease.

Worf: A therapeutic treatment of infected trees might be more readily approved than a preventive treatment.

Ryker: Benomyl has recently been registered for heavy soil drenches for containerized ornamentals. The effect of soil treatments on earthworms needs to be studied in more detail. The growth of grass is greatly improved by the treatment. We need more information on the biological changes that occur.

Shigo: All wounds made for repeated stem injections turn your tree into a sieve; they are going to cause you great trouble.

Chairman: Compare the treatment with an operation for cancer: without

it, the patient will die. Slime-flux from the heartwood (wetwood) can also be a problem, but it might be cured by adding an antibacterial substance to the injection fluid. Research on the effects of wounding are badly needed.

Schreiber: Soil type may have a major influence on the efficacy of soil treatments. Clay soils tend to adsorb the benomyl strongly, as does organic matter. Sandy soils are the best for uptake.

Hubbes: What is the effect of high-pressure injection on the fine structure of the living wood?

Chairman: This is not known.

Kondo: Good results were obtained in Ottawa during 1971, 72 and 73 with injection of MBC-phosphate into severed roots, using variable root adaptors. Attachment should be completed within 30 seconds after severing the root, to avoid air-embolism. Up to 200 imperial gallons were injected in large, mature trees (30-40 inch dbh) over a period of about 48 hours at a pressure of 10 psi. The concentration used was 250-500 ppm at pH of 4.2. Elms are apparently highly buffered (varying between 6.8 to 7.5). The active material appears to become confined to the xylem after 2 years. In the year of treatment, the material penetrates in the entire sapwood as well as in the phloem in smaller amounts. In the second and third year, new annual rings of wood and phloem are formed which remain free of the material. Root flares have been treated as well, but this led to a less even distribution throughout the tree. The best distribution was obtained by injecting in roots at some distance from the root collar. A remarkable phenomenon was the lush growth in the crown which appears in every treated tree in subsequent years. Much uptake could be obtained even prior to budbreak. In bioassays for checking the presence of the active material in parts of the tree, the fungus *Penicillium expansum*, appears to be very suitable. Results parallel those with *C. ulmi*. Before and after treatment, we assess the extent of symptom expression by means of a disease-index, expressed as the Tree Class x Proportion of crown affected x 100. It is suggested that the standard use by researchers of a uniform method of rating diseased elms would be of mutual benefit.

Ouellette: Will the fungus develop strains that are resistant to Benlate, as other fungi have?

Chairman: Eventually, yes. We may have other effective fungicides by that time. The injection method has opened up many new possibilities.

Burdekin: Let us see this method in its right perspective. It is expensive in material and labor. Failures have been reported, too. On healthy trees, as a preventive method, insecticides are cheaper and far more quickly applied. The treatments with these fungicides will make an important contribution mainly on trees which have already been infected. It is still poorly known how durable the effects are in these cases. A very important further improvement would be achieved if it were possible to save trees infected through root grafts.

RESEARCH ON CHEMICAL AND BIOLOGICAL CONTROLS FOR ELM BARK BEETLES

by JOHN W. PEACOCK, *Northeastern Forest Experiment Station, Forest Service, USDA, Delaware, Ohio 43015, U.S.A.*

THE SMALLER EUROPEAN elm bark beetle, *Scolytus multistriatus*, and the native elm bark beetle, *Hylurgopinus rufipes,* are the principal vectors of Dutch elm disease in North America. By inoculating healthy elms with the causal fungus, these two species have indirectly been responsible for the death of hundreds of thousands of elms worth many millions, perhaps billions, of dollars, and have extended the range of Dutch elm disease throughout most of the eastern two-thirds of the United States and southern Ontario, Quebec, and New Brunswick. All of this has occurred despite control efforts based on data from 40 years of research initiated about the time of the discovery of Dutch elm disease in symptomatic trees in Cleveland, Ohio, in 1930 (*May and Gravatt 1931*).

S. *multistriatus* is a species introduced from Europe and first reported in the United States in 1909 by Chapman (*1910*). It is the principal vector of Dutch elm disease in the United States and is currently reported in all of the contiguous 48 states except Arizona, Florida, and Montana (*Barger and Hock 1971*). It is also found in southern Ontario

(*Finnegan 1957*) where it is probably the most important vector of the disease. *H. rufipes* probably occurs throughout most of the natural range of the American elm, *Ulmus americana*, and is an important vector of Dutch elm disease in certain northern areas of the United States (*Collins 1941*). It is the principal vector of Dutch elm disease in Canada outside of southwestern Ontario.

Early research efforts on these two insects were aimed at defining their biology and describing their role in disease transmission. The biology of *S. multistriatus* in the United States was presented by Readio (*1935*) and by Wallace (*1940*). Wolfenbarger and Buchanan (*1939*) reported on its feeding behavior, which results in fungal inoculation. A complete report on the life history of *H. rufipes* was given by Kaston (*1939*). Collins (*1935*) reported on the role of this beetle in disease transmission, as did Thompson and Matthysse (*1972*).

In the late 1930s and early 1940s, limited Dutch elm disease control was achieved only where sanitation of diseased elm trees was practiced. After World War II, research on chemical control led to the development and use of the potent and highly effective insecticide DDT for control of the beetle vectors. This chemical, when used in conjunction with an efficient sanitation program, provided what proved to be the best tool for the limitation of Dutch elm disease losses to relatively low levels.

The banning of DDT in the late 1960s required the replacement of this insecticide in control programs with the chemically-related insecticide methoxychlor, which is an acceptable substitute for DDT because of its relatively low mammalian toxicity, its safety for birds and wildlife, and its biodegradability. Present recommendations for the control of Dutch elm disease call for spraying of elms just prior to bud break with an emulsified solution of methoxychlor (*Barger 1971*), coupled with a sanitation program to destroy beetle breeding sites.

In addition, the herbicide Vapam®[1] is recommended for destroying elm roots to prevent root-graft transmission of the disease organism where mature elms are planted within 10-m spacing (*Himelick and Neely 1965*). The early removal of single-branch infections may also be useful in eliminating the infection from beetle-inoculated elms, although this technique is often unsuccessful because the fungus is always present well before symptoms are expressed externally (*Campana, unpublished data*). Furthermore, this technique is useless on trees infected through root grafts, where disease development is usually systemic. Finally, recent studies indicate that the application of systemic fungicides such as Benlate® may be useful for the prevention of infection (*Hock et al. 1970, Biehn and Dimond 1971, Smalley 1971, Hart 1972, Gregory et al. 1973, Kondo and Huntley 1973, Stipes 1973*).

The integrated use of these control methods seems to be the best hope for achieving satisfactory disease control. Sanitation to remove beetle breeding sites is the most important component in any control program and must be practiced at all costs regardless of what other control options are used. Without an efficient sanitation program, the other control options listed will have a limited effect. The personnel, equipment, time, and cost requirements for insecticide spraying, Vapam treatment, pruning, and Benlate treatment may prohibit the use of one or all of these techniques in an area-wide disease control program. In fact, many cities have already found that these control options can be used only to protect a limited number of high-value trees. However, there is some hope that present research may yield new methods for the manipulation or reduction of beetle populations that could drastically increase the efficiency of beetle control procedures while decreasing manpower, equipment, and cost requirements. Some of this research is discussed in the following sections.

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[1]The use of trade names in this publication is for the information and convenience of the reader. It does not constitute an official endorsement or approval by the U.S. Department of Agriculture.

INSECTICIDES

Insecticides have been an important part of elm bark beetle control programs since Collins *et al.* (*1936*) first reported that beetles were killed after feeding on elm twig crotches treated with arsenicals. Arsenicals were used for beetle control until Whitten (*1945*) showed that DDT was more effective in preventing beetle feeding in the twig crotches of healthy elms. From the mid-40s to the late-60s, DDT was the insecticide most strongly recommended and most often used for elm bark beetle control. When used in conjunction with an efficient sanitation program, DDT gave control of the beetle vectors, thus allowing entire cities and individual homeowners to limit Dutch elm disease losses to relatively low levels. However, policies adopted in the United States in 1968 ended the use of DDT for elm bark beetle control. These policies were the result of continual pressure from environmental groups on federal, state, and municipal governments to ban DDT because of its long residual effect, resistance to degradation, and cumulative build-up in food chains.

Fortunately, some city governments were already using methoxychlor as a substitute for DDT even before 1968, and were claiming success in beetle control. Bromley (*1950*) had achieved promising results with methoxychlor as early as 1949. Doane (*1962*) found that methoxychlor produced a low mortality in beetles caged on treated elm twigs, but the average size of feeding scores indicated beetles did not feed extensively. Wootten (*1962*) concluded that where spray coverage was comparable, methoxychlor was fully as effective as DDT for beetle control. Barger (*1971*) confirmed the suitability of methoxychlor as a DDT substitute and methoxychlor is now the sole insecticide in use where an insecticide is part of a beetle control program.

Methoxychlor is suitable for use in elm bark beetle control because it is toxic to the beetle but lacks the objectionable

properties of DDT. From an environmental standpoint, its greatest assets are: (1) it is low in mammalian toxicity compared to DDT (5000-7000 mg/kg versus 87-500 mg/kg); (2) it is not stored in the fat tissue of warm-blooded animals; and (3) it is less toxic to birds and earthworms. Furthermore, it is rapidly degraded biologically to non-toxic metabolites.

There are a number of problems associated with the use of methoxychlor. Perhaps the most important is that city foresters and arborists question its ability to inhibit beetle feeding enough to reduce Dutch elm disease significantly in methoxychlor-treated areas. There is an explanation for the apparent discrepancy between the satisfactory control results of Barger (*1971*) and the poor results recorded in certain municipal Dutch elm disease control programs. Barger personally supervised the actual spray operations in his study and thus insured adequate coverage of each treated tree in the test area. Mist blower operators often do not cover mature elms adequately with methoxychlor and they are sometimes instructed to apply less than the recommended dosage because of high cost. DDT was more satisfactory than methoxychlor, even with poor application techniques, because it was much more toxic to beetles than methoxychlor. Of much greater significance, DDT deposits accumulated on treated elms from year to year increasing the total insecticide deposit. Methoxychlor degrades more rapidly. There are a number of other problems associated with the use of methoxychlor. Among these are: (1) it is toxic to fish, and fish mortality can occur where methoxychlor residues run off into fish habitats; (2) it is, like DDT, a chlorinated hydrocarbon, and is therefore believed by environmentalists to be capable of widespread environmental pollution; (3) it is expensive, costing nearly 3 to 4 times as much as DDT; and (4) its formulations cause damage to paint finishes on cars and aluminum house siding.

Obviously, if the use of insecticides in a beetle-control

program is to be continued, there should be research to find safer, less expensive, and more effective chemicals that could replace methoxychlor. Investigations could include studies on new and improved systemic and contact insecticides, and studies on the improvement of insecticide application techniques and insecticide formulations.

Systemic Insecticides

Systemic insecticides for elm bark beetle control were first investigated by Al-Azawi and Casida (*1958*). They found that demeton, dimefox, thimet, and Chipman R-6199 (Tetram®) were readily translocated in mature elms, but only Tetram gave control of *S. multistriatus.* Studies by Al-Azawi and Norris (*1959*) further demonstrated a reduction in the number of Dutch elm disease-infectible feeding niches resulting from treatment of elms with Tetram. However, after studying the hazards associated with the use of Tetram for beetle control, Al-Azawi, Norris, and Casida (*1961*) concluded that this chemical was so stable within elms and so toxic to non-target organisms that it could not be recommended for use in a Dutch elm disease control program.

In a study of two additional systemics, Bidrin® and phosphamidon, Norris (*1960*) found that Bidrin caused a significant decrease in feeding-niche length and a significant increase in mortality when *S. multistriatus* was exposed to twigs from treated elms (*U. rubra*). English and Hartstirn (*1962*) also reported a reduction in *S. multistriatus* feeding penetration to twig xylem after elms were injected with Bidrin. After additional field-testing of Bidrin and the development of Mauget®-injecting tools for implanting the insecticide in elms, Bidrin was recommended for use in Dutch elm disease control programs (*Shell Chem. Co. 1964*). However, a number of problems were associated with the use of Bidrin. These included: (1) phytotoxicity to treated trees at dosages

recommended for beetle control; (2) bark discoloration, splitting, and bleeding at the injection sites; and (3) excessive manpower, time, and cost requirements necessary for Bidrin injection. The problems associated with the use of Bidrin, coupled with conflicting reports on its effectiveness in preventing beetle feeding (*Butcher et al. 1966, Lincoln 1967, Lamdin et al. 1969*) resulted in discontinuance of its use for control of elm bark beetles.

At present, there is no extensive use of systemic insecticides for beetle control. However, if a safe, effective, easy to apply, nonphytotoxic systemic could be found, such a chemical could be used in an elm bark beetle control program for the protection of individual, high-value elms. These would probably be elms located on private property, not those treated as part of a municipal disease control program. It is unlikely that systemics could ever be used on a large scale for the protection of elms planted as street trees throughout a city because of the excessive manpower and funds required for such a program.

Contact Insecticides

It seems logical that safer, less expensive, and more effective contact insecticides can be found to replace methoxychlor for extensive spray programs on street trees. In past years a number of contact insecticides have been compared with DDT for elm bark beetle control. Matthysse (*1954*) studied dieldrin, lindane, parathion, chlordane, toxaphene, and methoxychlor in the laboratory and found that dieldrin, parathion, and lindane were equal or superior to DDT against bark beetles. Furthermore, treatment of elms by mist blower indicated that dieldrin was effective in the field as a residual insecticide against bark beetles at lower dosages than DDT. Doane (1958) compared dieldrin, heptachlor, lindane, and malathion with DDT applied to American elms. Dieldrin was as effective as DDT in killing beetles, but was less

effective than DDT in reducing feeding that reached the xylem of treated twigs. Lindane persisted well in the tests and compared favorably with DDT in prevention of twig feeding. Heptachlor and malathion were largely ineffective in preventing S. *multistriatus* feeding. Doane (*1962*) also compared the effectiveness of Thiodan®, Zectran,® and methoxychlor with that of DDT. Only Thiodan compared favorably with DDT in beetle mortality and prevention of beetle feeding.

Although these data indicate that dieldrin, lindane, and Thiodan might be effective for beetle control, none of these chemicals has been widely used in beetle control programs, primarily because of the potential hazards associated with their use.

Several new insecticides have recently been studied in laboratory tests where the chemicals were topically applied to S. *multistriatus* adults. Nineteen chemicals, including pyethroids, carbamates, organic phosphates, and chlorinated hydrocarbons were compared to methoxychlor. Four of these gave relatively good contact toxicity: N1A-24110, Landrin®, Imidan®, and carbofuran (*Lyon and Barger, unpublished data*). N1A-24110 is a synthetic pyrethroid that has little residual life, but apparently does have some systemic activity in plants. Landrin, a carbamate, has some toxicity to birds that would have to be considered in any field tests. Imidan is an organophosphorous insecticide and carbofuran, a carbamate. Carbofuran has a low dermal toxicity, but its fairly high oral toxicity to mammals could prevent its use in a beetle control program. These four insecticides will next be bioassayed in the laboratory using caged beetles confined to insecticide-treated twig crotches. If any one of them shows promise in these bioassays, it should then be evaluated in the field.

Insecticide Application and Formulations

The development of new application techniques or improved insecticide formulations might increase insecticide control of elm bark beetles. Research in this area should be aimed at increasing insecticide deposits in the canopy of mature elms, and at reducing manpower and equipment costs, environmental hazards, and other associated problems, such as the spotting of car paint finishes and aluminum siding.

For new methods in the application of systemic insecticides, an evaluation of pressure injection systems (similar to those being tried experimentally with Benlate) seems logical. Pressure injection would have several advantages over the Mauget-type injectors. More insecticide could be injected in a shorter time, thus reducing labor costs. Fewer holes would be required for introduction of chemical in the trunks of treated trees, thus reducing physical damage to the trees and further reducing expenses for labor. Finally, it would seem that pressure injection would provide better distribution of the chemical throughout the crown of large elms.

Spraying from helicopters has been studied (*Wallner and Leeling 1968, Wallner et al. 1969, Barger 1971, Barger et al. 1973, Cuthbert et al. 1973*) as a method of increasing the deposits of methoxychlor in the canopy of mature elms while reducing the time required for application. Despite the fact that helicopters provide a method of getting adequate insecticide deposits in the canopy of elms in less time than mist blowers and hydraulic sprayers, helicopter application has not received widespread acceptance because: (1) the cost of application is considered to be higher than that for mist blowers or hydraulic sprayers; (2) there are but a few days during which weather conditions are suitable for helicopter application; (3) there are strict regulations prohibiting low-level aircraft flights over some cities; (4) it is difficult, if not impossible, to prevent automobile movement in helicop-

ter-treated areas, with the danger of spotting of auto paint; (5) control of spray deposits is difficult with helicopter treatment; and (6) there is a greater pollution hazard from aerial application than from hydraulic spraying or mist blowing. Furthermore, Cuthbert *et al.* (*1973*) have shown that insecticide residues are insufficient to prevent beetle feeding in the lower branches and twigs of mature elms treated by helicopter.

Methoxychlor formulations have been the subject of two recent studies. Several commercially-available emulsifiable concentrate formulations of methoxychlor were evaluated by Cuthbert *et al.* (*1973*). Five different formulations were applied by helicopter, mist blower, and hydraulic sprayer to determine whether the type of formulation affected the initial or residual insecticide deposits. GLC analysis and bark beetle bioassays on treated elm twigs indicated no significant differences in insecticide residues related to the formulations tested, regardless of whether the carrier solvent was xylene or heavy aromatic naphthalene, whether the emulsifier was quick or slow-breaking, or whether white oil was added or not. However, there were significant differences in deposits related to application method: Hydraulic sprayer deposits were heaviest and most uniform (but twice as much insecticide was applied); deposits from mist blower application were almost as heavy as hydraulic, but deposits were highly variable; average helicopter deposits were one-half as heavy as from the other two methods. Deposits on tree tops were nearly the same for all three methods. No attempt was made to determine effects of the various formulations on Dutch elm disease incidence in the field, nor on car paint finishes.

Additional studies on methoxychlor formulations are the subject of a cooperative agreement between the U.S. Forest Service and the Cargill Company, Inc., of Minneapolis. The purpose of these studies is to determine whether methoxychlor can be formulated as a wettable powder or suspension to replace the present emulsifiable concentrate that uses

xylene as a carrier. The new formulations would eliminate the spotting of automobile finishes by xylene but they would require modification of conventional mist blowers to accept wettable powders and suspensions.

PARASITES AND OTHER BIOLOGICAL CONTROL AGENTS

Parasites

There have been a number of studies of the effects of hymenopterous parasites on elm bark beetle populations. Three indigenous hymenopterous parasites of S. *multistriatus* commonly occur in the U.S. : *Spathius benefactor*[2], a native braconid; *Cheiropachus colon*, a European pteromalid; and *Entedon leucogramma*, a European eulophid. In addition, a European braconid, *Dendrosoter protuberans*, has been introduced into the U.S. This species can be easily reared on S. *multistriatus* in the laboratory, can overwinter in Central U.S., and can reproduce itself under field conditions (*Kennedy 1970*).

All of these parasites except *E. leucogramma* oviposit through the bark onto beetle larvae, and thick bark can therefore reduce their efficiency. *E. leucogramma* enters the female beetle egg gallery and oviposits in the eggs, thus making it a more efficient parasite (at least with regard to oviposition) than the other three.

Percent parasitism of S. *multistriatus* in the field by these hymenoptera is extremely variable. Truchan (*1970*) reported that *E. leucogramma* and S. *benefactor* accounted for only 2 percent of the 96 percent beetle mortality he observed in an overwintering population of S. *multistriatus*. Williams (*1967*) found reductions in beetle populations by

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[2]The long association of the name S. *canadensis* with parasites reared from elm bark beetles was shown by Matthews (*1970*) to be erroneous. Most elm-reared specimens belong to the new species, S. *benefactor*.

S. *benefactor* up to 35 percent in shaded locations. Kennedy (*unpublished data*) reports parasitism of 43 percent of a sample population of S. *multistriatus* from southern Ohio; S. *benefactor* accounted for 72 percent and *E. leucogramma* for 27 percent of the parasitism.

D. protuberans is established in Wayne County, Michigan, apparently as the result of releases made by Butcher in 1968. This probably is the only successful release of *D. protuberans* in the U.S., despite numerous releases by Kennedy in Missouri and Ohio, and Truchan and Butcher in several areas of Michigan. There is a possibility that this parasite may also be established in Missouri, where Williams and Brown (*1969*) recovered individuals in 1967 from a 1966 field release.

A sample of a S. *multistriatus* population in Wayne County, Michigan, indicated 44 percent parasitism, with 21 percent due to *D. protuberans* and 77 percent due to *E. leucogramma* (*Kennedy, unpublished data*); S. *benefactor* was virtually absent from the parasite complex. Kennedy suggests that *D. protuberans* may have filled a niche previously occupied by S. *benefactor*.

Kaston (*1939*) reports S. *canadensis* (*benefactor* sp.n.) as the most common parasite of *H. rufipes* in Connecticut. Parasitism of *H. rufipes* by this braconid ranged from 5 to 75 percent, with average parasitism in the range of 5 to 10 percent.

Despite these numerous studies on parasites of elm bark beetles, several unanswered questions come to mind concerning their importance in the reduction of beetle populations. Among these are:

1. Can laboratory rearing and subsequent release of additional indigenous or imported parasites bring a significant reduction in beetle populations in areas where one or more of these parasite species is scarce or absent?
2. Are the indigenous species and *Dendrosoter* compatible in various ecological situations or, for example, does the absence of S. *benefactor* and the presence of *D. protuber-*

ans in some samples indicate that these two species are incompatible?

3. Would the release of indigenous or imported parasites be compatible with sanitation in a beetle control program? It is conceivable that parasites would reduce the population of beetles reproducing in diseased elms not removed in a sanitation program. Parasite releases and sanitation may be incompatible in that sanitation would destroy parasite as well as beetle populations.
4. Should there be an intensive search for additional foreign parasites of bark beetles that could be reared and released in North America, as has been done with *D. protuberans?*

Further research to provide answers to these questions could yield useful information regarding the practical value of parasites in a beetle control program.

Nematodes

Saunders and Norris (*1961*) report nematodes from 12 genera associated with *S. multistriatus*. Only one species, *Parasitaphelenchus oldhami* was parasitic (*P. oldhami* was first reported from the body cavity of *S. multistriatus* by Oldham (*1930*) in England). The nematode was found as larvae in the body cavity of adult beetles in every sample population of *S. multistriatus* investigated by Saunders and Norris. Incidence and magnitude of nema infestations were density-dependent in both the field and laboratory. Laboratory infestation ranged from 10 to 100 percent. In the field, infestation of beetles from areas of very heavy outbreaks of *S. multistriatus* ranged from 85 to 100 percent. In areas of low beetle infestation, the percentage of nema-infested beetles was as low as 10 percent. Saunders and Norris were unable to detect pathological effects on beetle populations nor were they able to detect significant differences in the number of offspring from beetles, whether they were 100 percent infested or free of nematodes. Valek (*1967*) also was unable

to demonstrate any detrimental effects of nematodes on *S. multistriatus*.

Kaston (*1939*) reported nematodes in the coelomic cavity of 80 percent of adult *H. rufipes* he examined, but none in larvae or pupae. Very few of the adults had smaller-than-normal gonads, indicating that nemas probably had little effect on beetle fertility.

Mites

Several mite species have been found associated with *S. multistriatus* and one, *Pyemotes scolyti*, is an external parasite of the beetle. The biology of this mite has been investigated by Beaver (*1967*) and Moser and Roton (*1972*). The effect of this mite on *S. multistriatus* populations has not been studied; hence, the importance of this or any other mite for the control of *S. multistriatus* remains to be determined.

Mites are often found associated with *H. rufipes* (*Kaston 1939*) but most are probably saprophytes. *Pediculoides dryas* was reported by Kaston as "apparently" parasitic, since it was seen eating eggs and larvae of the beetle. As is the case with *S. multistriatus*, there have been no studies on the importance of mites in reducing *H. rufipes* populations, and therefore their importance in beetle control is unknown.

Predators

Several predators attack *S. multistriatus*. Williams and Brown (1969) report the clerid, *Enoclerus nigripes* var. *dubius* attacking adult beetles in the field. *E. ichneumoneus* and *Tenebroides dubia* were also collected in association with *S. multistriatus* but predation was not actually observed. *E. nigripes* also attacks *H. rufipes* (*Kaston 1939*). Kaston observed a single adult *E. nigripes* consume five *H. rufipes* in succession. He further indicated that the absence of parent bark beetles, especially the male, from egg galleries is probably due to their having been eaten by this predator. Kaston

also states that *Platysoma coarctatum* is probably a predator of *H. rufipes* along with the fly *Lonchaea polita*, which is probably a facultative predator.

Woodpeckers have also been reported as *S. multistriatus* predators (*Wallace 1940, Truchan 1970*). Truchan observed three species, the red-headed, downy, and hairy, working on beetle-infested elms. Other workers have also recorded the attack of woodpeckers on infested elms, but no data have been published on the importance of woodpeckers in beetle mortality.

Nematodes, mites, and predators obviously must have some influence on natural populations of elm bark beetles, but they seem to have little effect on Dutch elm disease incidence. Furthermore, because difficulties would certainly be encountered in the mass production of these organisms, additional research leading to the rearing and release of nematodes, mites, or predators seems unwarranted.

Fungal and Bacterial Pathogens

There have been several studies reported on the effect of parasitic fungi and bacteria on the survival of *S. multistriatus*. Charles (*1941*) first recorded the occurrence of the muscardine fungus, *Beauvaria bassiana* on *S. multistriatus*. Doane (*1959*) found this fungus in beetle larvae from five widely-separated areas in Connecticut. Up to 6.5 percent of the overwintering larvae in trees cut from city streets were infected. In one epizootic caused by the fungus, 97 percent of larvae were killed in the bark of trees in a shady grove; less than 4 percent were killed in trees standing nearby in the open. In laboratory experiments 99 percent of fungus-treated larvae were killed in 5 days.

Since it appears that warm, moist weather conditions are necessary before epizootics of *Beauvaria* can occur (*Steinhaus 1954*), this pathogen would probably be of little value in an organized Dutch elm disease program. However, *Beauvaria* and other fungi are probably important beetle control agents

where the environment is suitable; e.g., in wooded or otherwise heavily-shaded locations.

Bacteria have been reported as pathogens of S. *multistriatus*. Pesson, Toumonoff, and Hararas (*1955*) first observed diseased larvae in laboratory cultures and isolated two new bacteria from those larvae: *Aerobacter scolyti* and *Escherichia klebsiellaeformis*. Doane (*1960*) studied these two bacteria and the bacterium *Serratia marcescens* for their effects on S. *multistriatus* larvae. Bacteria would seldom infect healthy larvae feeding on a bacteria-inoculated artificial feeding medium, but would infect injuries made by larvae biting each other on contact. Crowding of larvae in the artificial medium increased the number of bites and the efficiency of the bacteria as pathogens. Doane concluded that few beetle larvae would come in contact with each other, and hence the bacteria would be very inefficient pathogens, in any but an extremely heavy infestation of S. *multistriatus*. Populations of beetle larvae so large that the larvae attack each other are probably rare in nature.

Since some degree of success has been experimentally achieved in reducing beetle populations with fungi and bacteria in the laboratory, research to improve strains of existing pathogens or a search for new pathogens for practical beetle control could prove fruitful. This research could include studies on viral pathogens of elm bark beetles, an area that has been neglected to date.

FEEDING STIMULANTS AND DETERRENTS

One approach to the control of Dutch elm disease would be the reduction or elimination of beetle feeding on the twig crotches of healthy elms through the use of chemical feeding deterrents. Hastings and Beroza (*1961*) reported the first attempts to find a synthetic chemical deterrent that would inhibit S. *multistriatus* from feeding on elm twig crotches.

One hundred seventy-six candidate chemicals were assayed in laboratory tests, but none was a total or consistent deterrent over the entire test period (48 hours). However, one chemical, Ent. No. 3916 (bicyclo [2.2.1] hept-5-ene-2, 3-dicarboxylic acid, *cis*-, dimethyl ester), gave the most deterrence with no beetle mortality, and could be a true deterrent chemical. There have been no follow-up studies on this or any other potential synthetic deterrents.

Since feeding by *S. multistriatus* is restricted to the Ulmaceae, it is probable that naturally-occurring feeding inhibitors are present in the bark of non-host trees. If such inhibitors could be isolated, identified, and synthesized in large quantities, it is conceivable that these inhibitors could be used in a practical beetle control program. Considerable knowledge regarding the chemical basis for *S. multistriatus* feeding behavior on host and non-host trees is already available and should be of value in developing the practical use of deterrents.

In the field, adult beetles feed in the twig crotches of several species in the genus *Ulmus*, arriving at the feeding site as the result of random dispersal in the crowns of healthy trees (*Baker and Norris 1968*). In the laboratory, this insect also will feed extensively in twig crotches of *Zelcova serrata* but not on *Celtis occidentalis* (*Becker and Mankowsky 1965*). *S. multistriatus* probably does not feed on trees outside the Ulmaceae in nature, but Dixon (*1964*) reported that confined adults would feed on twig crotches of *Malus pumila, Crataegus* sp., *Quercus alba, Acer saccharinum, Pyrus communis,* and *Populus deltoides* when they had no choice. Crotch feeding was similar in all species, but usually of less depth than in *U. americana*. However, twig crotches from all of the above species (except *P. communis*) and from 25 other non-hosts were rejected in laboratory tests where the beetles were given a choice between twig crotches from these species and *U. americana* (*Peacock, unpublished data*).

Laboratory bioassays on host and non-host extracts com-

pare favorably with the aforementioned twig-crotch studies. Using a bioassay similar to that reported by Norris and Baker (*1967*) and modified by Doskotch, Chatterji, and Peacock (*1970*), it has been determined that ethanolic extracts of twig bark from *U. fulva, U. pumila*, and *Z. serrata* stimulate feeding almost as well as extracts from *U. americana* (*Peacock, unpublished data*). Gilbert, Baker, and Norris (*1967*) reported that benzene extracts of *Fraxinus americana, M. pumila*, and *P. tremuloides* also stimulate adult feeding, even though the beetles do not feed on these species under natural conditions.

The acceptability of *Ulmus* for feeding and the stimulatory activity of extracts from *Ulmus* twig bark are due to chemical feeding stimulants contained in the bark. Two of these stimulants have been isolated and identified as (+)-catechin 5-β-D-xylopyranoside and lupeyl cerotate (*Doskotch et al. 1970*). (Lupeyl cerotate may be the same compound as the triterpene reported by Baker and Norris, 1967). The structure of the glycoside was reinvestigated and in a paper by Doskotch, Mikhail, and Chatterji (*1973*), and revised structure (+)-catechin 7-β-D-xylopyranoside was given. Although the glycoside and lupeyl cerotate are both somewhat stimulatory by themselves, a mixture of the two is necessary to achieve about 70 percent of the activity of the ethanolic extract of *Ulmus* twig bark. Catechol (*Borg and Norris 1971*) and p-hydroxybenzaldehyde (*Baker et al. 1968*) have also been reported as *S. multistriatus* feeding stimulants, but neither of these compounds was isolated from *Ulmus* twig bark.

Trees not fed on by *S. multistriatus* can be grouped in two categories with regard to the response of beetles to chemicals contained in the bark: (1) Those trees that are unacceptable for beetle feeding because their bark contains chemical feeding deterrents (or repellents or both), and (2) those trees that are unacceptable because their bark is chemically neutral with respect to beetle feeding; i.e., it contains neither

stimulants nor deterrents. In addition, certain non-host trees are probably unacceptable for physical reasons, such as bark texture.

To date, the only naturally-occurring feeding inhibitor that has been isolated and identified from a non-host of *S. multistriatus* is juglone (5-hydroxy-1, 4-naphthoquinone) from the bark of *Carya ovata* (*Gilbert et al. 1967*). Norris (*1969*) has also found that other substituted naphthoquinones, in addition to juglone, will deter feeding and suggests that feeding stimulation and inhibition is the result of a quinone-quinol (oxidation-reduction) transduction of stimulant energy from olfactory and gustatory chemicals into the nervous system of the beetle (*Norris et al. 1970*).

There is evidence that feeding deterrents can be isolated and identified from other non-host trees since extracts from the bark of several other trees in addition to *C. ovata* will also inhibit beetle feeding in the laboratory. An extract of *Q. alba* twig bark deters feeding (*Gilbert and Norris 1968*) as do ethanolic extracts from the bark of *Q. velutina*, *Q. prinus*, *Q. palustris*, *Q. imbricaria*, *Q. bicolor*, *Ailanthus altissima*, *Tilia americana*, *P. deltoides*, *C. cordiformis*, *A. saccharinum*, *A. saccharum*, *Morus alba*, *Maclura pomifera*, *Pinus sylvestris*, and *Juglans nigra* (*Peacock, unpublished data*). A cooperative study by the Department of Pharmacy of The Ohio State University and the U. S. Forest Service is presently in progress to isolate and identify the deterrents in *A. saccharinum*, *Q. prinus*, *Q. palustris*, and *J. nigra*.

Feeding by *H. rufipes* is also restricted to the Ulmaceae. Unlike *S. multistriatus*, however, *H. rufipes* rarely feeds in twig crotches of healthy trees; it feeds most often on the trunk and branches greater than 2.5 cm in diameter (*Kaston and Riggs 1938*). Trunk feeding occurs on small elms when beetles extend their hibernation tunnels deeper into the thin bark on the trunks. Feeding on branches results from a second feeding period in the thin bark of 5-to-10-cm branches, after the beetles have emerged from hibernation

cells in the thick bark of trunks and larger branches (*Thompson and Matthysse 1972*).

The preference for Ulmaceae and the rejection of non-hosts by *H. rufipes* must be due in part to the presence of naturally-occurring feeding stimulants and feeding deterrents. Little information has been published on the feeding behavior of *H. rufipes*. Borg and Norris (*1969*) studied its response to benzene and ethanol extracts of *U. americana* trunk bark in the laboratory. *H. rufipes* adults would not feed on the benzene extract of trunk bark or on p-hydroxybenzaldehyde (both of which stimulate feeding by *S. multistriatus*), but were stimulated to feed on an 80 percent ethanol extract of bark.

There have been no reported attempts to study synthetic or natural deterrents of *H. rufipes*. It seems likely that feeding deterrents could be chemically isolated and identified from non-host tissues, utilizing techniques similar to those used successfully for *S. multistriatus*. Deterrent fractions could be compared with the bioassay of Borg and Norris (*1969*). Furthermore, the practical use of deterrents to control feeding by this beetle would seem to be as promising as for *S. multistriatus*, or more so. Because *H. rufipes* feeds primarily on the trunks and larger branches of healthy elms, application of deterrents would be less difficult than for *S. multistriatus*, where there must be complete coverage of all feeding sites in the entire crown.

What is the potential for the practical use of feeding deterrents in a bark beetle control program? If potent feeding inhibitors can be found and a method of applying them can be devised, then feeding inhibitors could be used as a substitute for or as a supplement to insecticides for the protection of high-value elms. Since naturally-occurring feeding inhibitors would most likely be relatively non-toxic and therefore harmless to non-target organisms in the environment, their use could conceivably eliminate the hazards associated with the application of toxic insecticides.

The most formidable task ahead does not seem to be the isolation and identification of feeding deterrents, but rather the development of inexpensive, efficient methods of applying them that will result in long-lasting, highly potent deposits of deterrents in the crowns of mature elms. Application techniques that might be successful are the pressure injection of deterrents into the xylem of healthy trees and the mist blower application of deterrents mixed with a sticker.

ATTRACTANTS (PHEROMONES)

S. *multistriatus* adults are attracted to the declining elms in which they breed by primary, host-produced odors (*Meyer and Norris 1967a*) and by beetle-produced pheromones (*Peacock et al. 1971*). Pioneer beetles of both sexes are initially attracted by the relatively weak primary host attractants produced in declining elm tissue. These primary attractants have not yet been isolated and identified from host tissues, but Meyer and Norris (*1967b*) report that two major products of oxidative degradation of hardwood lignin, vanillin and syringaldehyde, will elicit a response from walking beetles in a laboratory olfactometer. There have been no reported attempts to assay these chemicals in the field.

Virgin female beetles, initially attracted to elm tissue by host attractants, produce a powerful pheromone that is responsible for the mass attack of males and females on suitable breeding material. Males do not produce the pheromone, nor do mated females (*Peacock et al. 1971*). Apparently females simply cease pheromone production after mating because laboratory and field tests have demonstrated that neither sex produces an antipheromone (*Bartels and Lanier 1974*). The U.S. Forest Service and the Departments of Forest Entomology and Forest Chemistry of the State University College of Forestry at Syracuse University are presently cooperating in efforts to isolate and identify the S. *multistriatus* pheromone.

Laboratory bioassays with walking male beetles indicate that at least part of the pheromone "bouquet" is contained in frass produced by virgin female beetles and that the pheromone can be removed from the frass by solvent extraction with pentane or benzene (*Peacock et al. 1973*). Furthermore, several GLC fractions from frass extracts will elicit responses from male beetles in the laboratory. However, neither frass nor frass extracts will attract flying beetles in the field. This indicates that frass apparently does not contain all of the pheromone chemicals required for beetle attraction, or that one or more of these chemicals is lost through volatilization from the surface of the fecal pellets shortly after the frass is produced.

We have recently demonstrated, in a study not yet published, that an extract of the volatiles from air surrounding female beetles boring in elm bolts will elicit a positive response from walking male beetles in the laboratory and, more importantly, will attract wild, flying beetles in the field.[3] This extract, which apparently contains all of the chemical constituents of the pheromone, has been fractionated by GLC and the resulting fractions have been tested in the laboratory and in the field. We have arrived at the tentative conclusion that at least three chemicals, acting in combination, are required for maximum attraction in the field. There is evidence that at least two of these chemicals are produced by the virgin female beetle. Studies are now in progress to identify the active compounds and synthesize an attractant mixture.[4]

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[3]Peacock, J.W., R.A. Cuthbert, W.E. Gore, G.N. Lanier, G.T. Pearce, and R.M Silverstein. 1975 Collection on Porapak Q of the aggregation pheromone of *Scolytus multistriatus* (Coleoptera: Scolytidae). J. Chem. Ecol. 1: 149-160.

[4]The three components of the *S. multistriatus* pheromone have been isolated, identified, and artificially synthesized. The chemicals are α-cubebene, 4-methyl-3-heptanol, and 2, 4-dimethyl-5-ethyl-6, 8-dioxabicyclo (3.2.1) octane (multistriatin). The attractant activity of a synthetic mixture of these three chemicals, "Multilure", was confirmed in field studies in 1974. See Pearce, G.T., W.E. Gore, R.M. Silverstein, J.W. Peacock, R.A. Cuthbert, G.N. Lanier, and J.B. Simeone. 1975. Chemical attractants for smaller European elm bark beetle, *Scolytus multistriatus* (Coleoptera: Scolytidae). J. Chem. Ecol. 1: 115-124.

As a corollary to these chemical studies, we are starting to study the patterns of emergence, dispersal, and mating of this insect, and to develop attractant delivery systems and improved traps. A delivery system must be developed that will permit the release of attractant to give maximum potency over the entire beetle flight season (May to October). Glass capillary tubes and plastic containers are presently being investigated for use as reservoirs for attractant chemicals in the traps. It may be necessary to incorporate non-volatile "keepers" in the attractant mixture to prevent too-rapid volatilization.

A trap must be developed that will be inexpensive, easily deployed, and effective in trapping and killing large numbers of beetles over an entire season. We have yet to determine where the traps should be positioned, whether on elm trees or some other site. Preliminary data from our studies indicate that beetles responding to attractant-baited traps placed on the trunk of an elm tree, will sometimes feed in the twig crotches of that tree before they alight on the trap. Such feeding could result in inoculation of healthy elms with the Dutch elm disease pathogen. If this type of feeding proves to be significant, i.e., if trees with traps become diseased more often than those without, then some other trap location will be necessary.

The vertical distribution of traps must also be investigated. To date, all trapping of S. *multistriatus* with attractants has been with traps at 1.5 and 3 m above the ground. We have yet to determine if traps would be more effective at greater heights (e.g., in the canopy of mature elms), or at several different heights.

Use of attractants for trapping and killing S. *multistriatus* in urban and suburban situations holds much promise. We already know that in Detroit, Michigan, large numbers of beetles were attracted to and killed at traps containing virgin females tunneling in elm bolts (Cuthbert, unpublished data). Furthermore, we have evidence that crude extracts

containing volatiles from the air surrounding tunneling females are as potent as the female-elm bolt combination. There is reason to believe that synthetic attractants will be as attractive as the crude extract, or more so. Assuming that a satisfactory delivery and trap system can be developed, it should be possible to trap and kill a large portion of the *S. multistriatus* population in any given area.

In addition to lethal trapping of beetles with attractants, two other techniques come to mind: (1) the synthetic attractant could possibly reduce successful beetle matings by inhibiting the ability of males to find virgin females; or (2) the attractant could be used to lure beetles to chemosterilants contained in nonlethal traps.

The use of attractants for control of *S. multistriatus* has certain advantages over attractants used for the control of other insect pests, such as forest insects and insects attacking extensively-planted crops. Among these advantages are:

1. Elms planted along city streets allow easy access for trap placement and trap servicing at any height or distance between traps.
2. *S. multistriatus* is an aggregating insect and thus traps do not have to compete with individual females as is the case with some other pests such as pink bollworm, gypsy moth, etc. Furthermore, both males and females can be attracted to and killed at attractant-baited traps. This provides the obvious advantage of eliminating both sexes as vectors (which also indirectly eliminates potential brood sites) while at the same time directly reducing the number of beetles in subsequent broods by killing the females.

There are several foreseeable problems in the use of attractants in a *S. multistriatus* control program. Migration of beetles into trapping areas may be a problem in some urban and suburban situations, where there is an influx of beetles from other locations where no beetle control is practiced, such as woodlots and along streams. However, preliminary

data from trapping studies in Detroit indicate that most beetles do not fly long distances in response to attractive odors after emergence from brood material. Thus, migration of beetles into trapping areas may be relatively unimportant.

Serious problems may be encountered in attempts to use attractants in areas of high Dutch elm disease incidence, especially where no other beetle control methods are practiced. It may be possible to develop and deploy large numbers of unobtrusive attractant traps, capable of trapping and killing the extremely large number of beetles that exist under these conditions, but it seems improbable, because of competition from many diseased trees, that beetle numbers could be reduced to a level low enough to bring about significant reductions in beetle-vectored cases of Dutch elm disease.

Finally, we can foresee problems in measuring the success or failure of an attractant trapping program. A statistically significant reduction in Dutch elm disease losses in trapping areas versus losses in check areas would provide the most meaningful indication of success, but differences in tree losses would be difficult to measure in areas of low disease incidence, where the attractants have the best chance for success. Measurement of such small differences in tree losses (which may be as low as 1 to 3 percent) will be further complicated by delays in disease symptom expression and by local variation in disease rates.

There are no published reports of research on *H. rufipes* pheromones. A pheromone must certainly be involved in breeding site selection by this insect and it would seem that research on this aspect of the insect's behavior could possibly lead to the development of a practical control method. The same advantages over other control methods noted for *S. multistriatus* would probably apply to *H. rufipes.*

H. rufipes is attracted in small numbers to traps containing virgin female *S. multistriatus* tunneling in wood, probably in response to host odors liberated from the decaying elm bolts by the tunneling females. But *H. rufipes* is not

attracted to the active GLC fractions that attract flying S. *multistriatus* (*Peacock, unpublished data*). Most likely, *H. rufipes* produces a pheromone that is chemically unlike that produced by S. *multistriatus*; however, the same host-produced primary attractants may be involved in breeding-site selection by both insects.

MALE STERILIZATION

Sterilization of male elm bark beetles, whether by chemicals or X-rays, has received little attention. Chemosterilants could conceivably be used in conjunction with attractants to lure flying beetles to non-lethal traps. Males sterilized in the traps could then leave the traps and mate with wild females at breeding sites.

The mating behavior of S. *multistriatus* appears to be such that male sterilization could be used to reduce beetle populations, i.e., females usually mate with only one male, but males mate with several different females. There have been conflicting reports in the past concerning the number of times males and females mate, but Bartels and Lanier (*1974*) have shown that a single male S. *multistriatus* can mate with as many as 31 virgin females in the laboratory. Although males probably fertilize fewer females under natural conditions, facultative polygamy is probably the rule in this species. This behavioral characteristic coupled with the fact that females are no longer attractive after mating (Peacock et al. 1971) indicates: (1) that several females could be rendered infertile by a single sterilized male; and (2) that a female rendered infertile by mating with a sterile male would not subsequently mate with fertile males.

To date, only Jorgenson (*1967*) has reported sterilization of S. *multistriatus* by chemical or other means. Jorgenson stated that he was able to achieve successful sterilization of males by bathing the adults in a 1 percent solution of Mapho®. There have been no follow-up studies on Mapho,

but several additional chemosterilants have been laboratory-tested on S. *multistriatus* (Cannon, unpublished data). These and other compounds having insect-sterilizing capabilities will be subjected to further laboratory and field testing, first to find sterilizing chemicals, and then to determine their long-term effectiveness, compatibility with attractants, and safety for non-target organisms.

SUMMARY

The ultimate goal in elm bark beetle research should be to provide a number of practical methods for use in an *integrated* control program. Such a program must include sanitation as its primary and most important component and should be compatible with existing procedures for disease control. New methods to complement sanitation in an integrated beetle control program may result from research now in progress and could include the use of: (1) new and improved safe and effective insecticides; (2) biological control agents such as parasites and beetle pathogens; (3) chemical feeding inhibitors; (4) attractants; and (5) chemosterilants.

Current insecticide studies may provide improved formulations of methoxychlor, or even new insecticides, which would be safer, less expensive, and more effective than methoxychlor as it is presently recommended for the protection of elms on an area-wide scale. Pressure injection techniques, similar to those presently being investigated for the application of systemic fungicides, may offer useful techniques for the protection of individual, high-value elms with systemic insecticides.

Studies on indigenous and imported hymenopterous parasites may determine the potential use of such bio-agents in a beetle control program, especially as an adjunct to existing sanitation practices. Future studies should include research

on the effects of bacteria, viruses, and fungi on beetle populations.

The isolation and identification of the natural product, juglone, a feeding deterrent from a nonhost tree of S. *multistriatus*, may be a first step in the development of methods for the use of such feeding deterrents for preventing beetle feeding in healthy elms. Additional research is needed to determine if such inhibitors can be used to give a long-lasting, inexpensive, safe control procedure that could replace or supplement insecticides for the protection of selected individual, high-value elms.

Elm bark beetle attractants offer the most promising new approach for the control or manipulation of beetle populations. Results of studies to date on attractants for S. *multistriatus* are encouraging. At least three chemicals attractive to elm bark beetles have been isolated and identified, two of these three have been artificially synthesized, and synthesis of the third component appears close at hand.[4] Two of the three compounds are apparently beetle-produced. A mixture of these three chemicals is almost as attractive as virgin females tunneling in elm bolts. If a synthetic attractant mixture proves to be effective in reducing beetle populations to levels low enough to bring about a corresponding significant reduction in Dutch elm disease incidence, it is possible that attractants could be used as a replacement for insecticides in conjunction with sanitation for the control of beetles, especially in areas of low disease incidence.

Other approaches to beetle control, such as chemosterilants or growth-regulating hormones, could conceivably be useful in an integrated beetle control program, but as yet there are insufficient data to predict their effectiveness in such a program.

The outlook for the control of Dutch elm disease is more promising now than at any time in the long history of this disease. Several new control options may soon be available for use in integrated disease and beetle control programs. In the

next few years, attractants, parasite releases, improved insecticides, and improved insecticide application methods will be evaluated for beetle control. Control methods that might be evaluated in the more distant future could include the use of feeding inhibitors for treatment of selected trees, and chemosterilants for use in conjunction with attractants.

If any of these new approaches are shown to have individual merit, they will then be evaluated in combination with other existing options to determine the cost and benefits of various combinations. City foresters and arborists could then determine what control option, or combination of options, would be used to protect individual trees, or street trees on a city-wide basis, depending on their available resources, including manpower, equipment, and funds, and the value of the trees to be protected.

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DISCUSSION

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Dr. Peacock has presented an excellent review of the entomological research related to DED done in the recent past and currently under way, particularly in the United States. The following is not a verbatim account of the discussion but is rather my summation of the main points raised in it.

Insecticides

The discussion on insecticidal control of elm bark beetles naturally centered on the effectiveness of methoxychlor in relation to DDT. The insecticide DDT is no longer used for elm beetle control either in the U.S. or in Canada. Methoxychlor has been used by the National Parks Service in Washington, D. C., since the mid-1950s as a replacement for DDT and in fact was substituted before DDT was phased out. Application is by mistblower at a concentration of 6 percent, with results just as effective as DDT. The point was raised that perhaps methoxychlor was not as quick-acting as DDT, and this permitted some penetration to the xylem by feeding beetles before they succumbed. This might be more important in the case of *Hylurgopinus rufipes*, as it has been found at Sault St. Marie that feeding niches made by this insect do extend to the xylem on sprayed trees.

There was lengthy discussion on the apparent discrepancies between the degree of success claimed for DDT and that achieved using methoxychlor. The evidence for the effectiveness of methoxychlor is provided by controlled experiments where great care was taken to apply the stipulated quantities of material. Application in practice may not achieve the same standards, and failures in control may follow.

There was a suggestion that DDT persisted for a number of years after application, and that the apparent early success of methoxychlor might be attributed to a carryover of DDT.

Dr. Peacock reported that cacodylic acid, Metasystox-R®, and 2-4-D had been tested in the United States as a means of either rendering elm material unsuitable for breeding material or killing beetles or both. Cacodylic acid was effective in doing both. The purpose underlying this method of control was to reduce breeding material and beetle populations in areas where it was too expensive to remove diseased trees. This same approach was being investigated at Great Lakes Forest Research Centre, Sault Ste. Marie, with the native elm bark beetle rather than S. *multistriatus*. Results to date, however, have not been successful.

In Canada, trees killed by cacodylic acid introduced into ax frills at the base become extremely attractive to flying *H. rufipes* beetles. Brood development is reduced in the lower part of the trunk, but proceeds normally in the upper parts of the tree. In the U. S., the acid was pressure-injected into the trunk, and this difference in technique as well as the different

bark beetle species may account for the difference in result achieved. The most striking result in the Canadian tests was the production of a very attractive trap tree.

Biological Control Agents

Biological control of bark beetle vectors in the U.S. and Canada has been unsuccessful. Most recently introductions of *Dendrosoter protuberans* have been made into the U.S., and the parasite is now established in the Detroit area of Michigan. There has been no measure of its efficiency. The same parasite was imported from Austria to Sault Ste. Marie in 1972, and it was successfully reared on the native elm bark beetle even though the parent stock was species of *Scolytus*. No parasites survived above snow level during the 1972-73 winter, but this experiment will be repeated to check on the technique used. No recoveries were made from two field releases near Sault Ste. Marie. On behalf of the Canadian Forestry Service, the Commonwealth Institute of Biological Control searched for pathogens of DED vectors in Europe and evaluated the effectiveness of parasites and predators. No pathogens were found and no conclusive evidence that parasites and predators were effective could be established. It was suggested that a search for parasites might be made in Japan.

The possible use of viruses, bacteria, and fungi was discussed, but no one present could provide any information that would suggest that biological control showed any promise. Problems relating to the fate of parasites and predators in areas where a sanitation program was conducted were discussed briefly. However, until such time as a promising control agent does appear, these related problems are academic.

Feeding Stimulants and Deterrents

The current position in relation to this topic is well covered in Dr. Peacock's paper. Discussion centered on elaboration of some of the points, and there was general agreement that a search for an effective deterrent or repellent, either natural or synthetic, would be a fruitful approach. There is a considerable amount of basic data available on the feeding response, particularly of S. *multistriatus*, but we are seeking a deterrent that would be used in place of insecticides. So far juglone is the only natural deterrent that has been isolated and identified. Small-scale preliminary field trials of a water-soluble form of this compound against S. *multistriatus* demonstrated that beetles were deterred from feeding on treated elm twigs. Study is proceeding on isolation and identification of other possible deterrents from non-host trees along with further studies on juglone derivatives.

The preliminary work at Great Lakes Forest Research Centre on the response of *H. rufipes* to extracts of elm bark was discussed. Results to date are quite inconclusive, but the search for a suitable deterrent to feeding by this species would appear to offer some possibilities for a future control mechanism.

Pheromones

Dr. Peacock described the research work done at the U.S.F.S. laboratory at Delaware, Ohio, and the cooperative program with the State University of New York College of Forestry. Virgin female beetles boring in elm wood produce a potent pheromone that is attractive to beetles in the field. The major part of the discussion centered on the best means of exploiting a synthetic pheromone when it becomes available. There were numerous problems still to be solved.

It could be used as a survey tool, and this is probably the simplest applied use. The use of traps baited with this attractant to bring in and kill large numbers of beetles is an obvious method to consider, but this in turn poses a number of problems that will require solutions. A suitable delivery system that will release the required amount of chemical for a sufficiently long period is needed. The most effective disposition of traps is yet unknown. Clearly large numbers of beetles should not be attracted into tree crowns where they could possibly inoculate the tree before being caught in the trap.

There was considerable discussion on whether it was possible to make a significant reduction in the number of beetles in an area. It would be difficult to assess what proportion of the total beetle population present in an area had been trapped and also to determine what reduction in disease incidence has been effected by the trapping.

It was agreed that the attack on the DED problem should be an integrated approach, using all weapons available against the pathogen and the vectors. With this premise, any significant reduction in beetle population achieved indirectly by the removal of potential breeding material or directly by capturing flying beetles is a progressive step.

VARIATION IN CERATOCYSTIS ULMI: SIGNIFICANCE OF THE AGGRESSIVE AND NONAGGRESSIVE STRAINS

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FOR MUCH of the fifty years since Bea Schwarz first described the causal organism of Dutch elm disease (*Schwarz 1922*), work on variation in *Ceratocystis ulmi*, and in particular work on variation in pathogenicity, has been a somewhat neglected field of research, especially when one considers the extensive literature produced on other aspects of the problem. A full review would not be appropriate here, as this is intended to be a look forward rather than a look back. Indeed Holmes (*1968*) has recently surveyed mycological aspects of the fungus in some detail. Nevertheless reference must be made to some key pieces of work; in particular that of Walter (*1937*) on cultural variation in *C. ulmi*, Buisman (1932) on the existence of sexual strains, Shafer and Liming (*1950*) on variation in compatibility type, and more recently Holmes (*1965*) on variation in pathogenicity among single ascospore isolates.

Our own active involvement in the problem began in 1971 when it became clear that a major epidemic of Dutch elm disease was developing in southern Britain. Inoculation

experiments showed that the form of the fungus associated with this epidemic was more aggressive than isolates obtained elsewhere in Great Britain (*Gibbs et al. 1972*). Further research (*Gibbs and Brasier 1973*) showed that two distinct groups of isolates were involved. The isolates of one group, termed *fluffy*, were fast-growing in culture with aerial mycelium aggregated into radial strands. Isolates of the second group were slow-growing, the majority with a *waxy* yeast-like appearance. There was virtually no overlap between the two groups on the basis of growth rate, and the great majority of isolates could be typed on this character alone.

An examination of the connection between cultural characters and pathogenicity was made in a comparative growth rate and inoculation experiment with 50 isolates, 30 *fluffy* and 20 *waxy*, from a number of geographical locations in southern Britain. Radial growth rates of the isolates were measured on 2-percent Oxoid malt extract agar at 18°C, and in pathogenicity tests 4-year-old clonal rooted cuttings of *Ulmus procera* were inoculated with spore suspensions of the isolates. In the results a complete separation of the two groups—*fluffy* aggressive and *waxy* nonaggressive—on the basis of growth rate and pathogenicity, was evident. It should be emphasized that the term nonaggressive is not used to mean that the strain is nonpathogenic, but rather that it has less ability to cause disease than the aggressive strain.

This correlation between cultural characters and pathogenicity enabled us to make a preliminary assessment of the relative frequency of the two strains, fluffy and waxy, in different disease situations in Britain. Samples showed that both strains were present in the chief outbreak areas, with the fluffy strain predominant; in other areas only the waxy strain was found. We then went on to examine a number of cultures from different parts of the world. In the Netherlands and other parts of Northwest Europe the waxy form of the fungus was found to be predominant. Cultures from North

America showed that both fluffy and waxy forms were present (*Gibbs and Brasier 1973*).

Origin of the Aggressive Strain in Britain

The discovery of the two strains of *C. ulmi* presented a question about the origin of the aggressive strain in the current epidemic. There seemed to be three possibilities. One was that an aggressive strain had survived from the previous epidemic in the 1930s. However, in view of the lethal behavior of this strain, this seemed an unlikely occurrence. We felt that there were two more probable alternatives: either that the aggressive strain arose by genetic change within an endemic nonaggressive gene pool, or that it was introduced to Britain.

The separation of *C. ulmi* into two groups, apparently without a range of intermediates, could be reconciled with either alternative if one assumed a rapid clonal build-up of the aggressive strain within the *C. ulmi* population once it had appeared. The close morphological and pathological similarity which we had discovered between the British aggressive and some North American isolates also suggested introduction, but could be reconciled with the theory of genetic change if a functional relationship were to exist between fluffy culture type and aggressiveness. Data from disease distribution were also inconclusive but tended to favor an origin by introduction. In the end very strong evidence for introduction was obtained in the discovery that rock elm logs from Canada infected with the aggressive strain of the fungus were arriving at British ports (*Brasier and Gibbs 1973*).

Identification of Aggressive and Nonaggressive Isolates in Culture

Our interpretation of the available data is that two groups of *C. ulmi* predominate in nature. One is aggressive, fast-growing (c. 3.2 to 4.8 mm per day at 18°C on 2-percent Oxoid malt extract agar), and with aerial mycelium aggregated into radial strands giving the culture a characteristic fibrous striate appearance (fig. 1,A). Clear zone lines are formed in response to diurnal fluctuation in light. Aggressive isolates are of remarkably uniform appearance even when cultures from diverse geographical origins are compared. The other group is nonaggressive, slower-growing (c. 2.0 to 3.1 mm per day), and more variable in morphology. Some isolates have a completely smooth waxy appearance with virtually no aerial mycelium (fig. 1,B). In others the waxy character may be masked to a greater or lesser extent by aerial mycelium, which may be somewhat aggregated into strands (fig. 1,C) or be present as an undifferentiated lawn of hyphae (fig. 1,D). Nonaggressive isolates with moderate or fairly profuse aerial mycelium may show some diurnal zonation, but this is not usually so striking as in the aggressive strain.

It must be emphasized that this classification applies only to fresh isolates. Cultural change in *C. ulmi* is well documented, especially by Walter (*1937*), who noted not only a marked tendency to sectoring in some cultures, but also a general tendency of all stock cultures to become more mycelial. At Alice Holt, where we maintain a large collection of isolates derived from single conidia, we often observe changes

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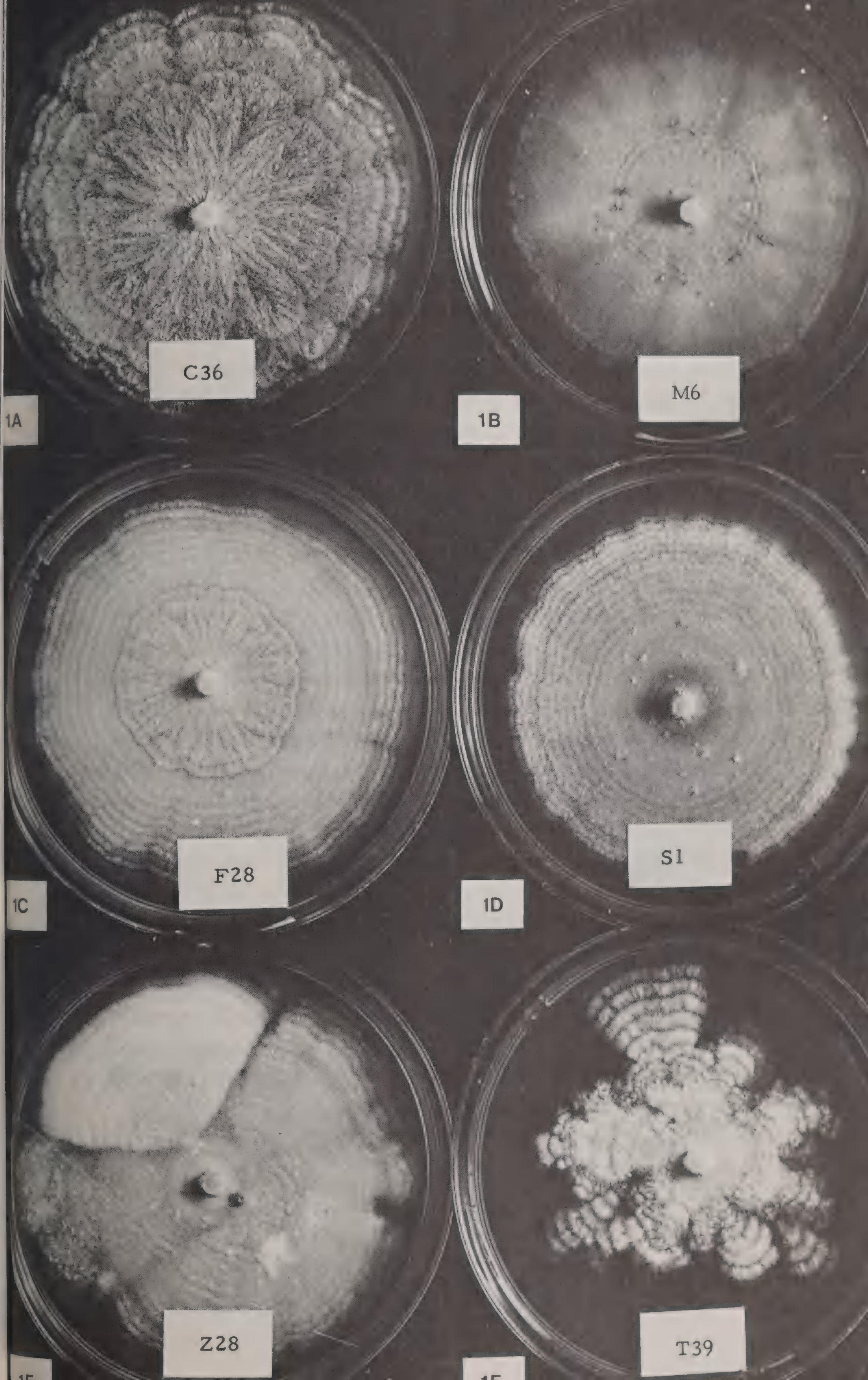
Figure 1.—Cultures of C. *ulmi* grown on 2-percent Oxoid Malt Extract agar for 7 days in darkness at 18°C followed by exposure to normal daylight. *A*, Typical fluffy aggressive isolate. *B*, Nonaggressive isolate with extreme waxy appearance. C, Nonaggressive isolate with sparse aerial mycelium, slightly differentiated into radial strands. *D*, Nonaggressive isolate with undifferentiated lawn of aerial mycelium. *E*, Sectoring nonaggressive isolate. *F*, Aggressive isolate that has degenerated to amoeboid type.


C36
1A
M6
1B
F28
1C
S1
1D
Z28
T39

in the phenotype of cultures over a period of time, not only the formation of sectors within a culture, but occasionally a complete change of appearance on transfer, when a sector type has been inadvertently selected. Nonaggressive isolates are sometimes very irregular, producing patches and sectors of various morphological types (fig. 1,E), some of them similar to those described by Walter (*1937*). Aggressive cultures also sector, often to a more profusely mycelial type. Occasionally they degenerate to a ragged slow-growing form that we call "amoeboid" (fig. 1,F).

Isolates of both types may change markedly if kept under mineral oil, and for this reason we prefer to maintain duplicate stock cultures in elm twigs at —15°C and in sealed malt agar plates at 2°C. Although we have examined many cultures, we have not observed a fluffy sector to emerge from a waxy culture, nor a waxy sector emerge in a fluffy culture.

The unstable nature of many *C. ulmi* cultures is probably attributable in part to mutation, but it is also suggestive of cytoplasmic instability, segregation of aneuploid nuclei, or other aberrant chromosomal behavior. Although cytological investigation has indicated that both aggressive and nonaggressive strains are regularly uninucleate (*Sansome and Brasier 1973*), this does not exclude the possibility that heterokaryosis is involved in cultural instability.

The medium used and the conditions of growth are important in enabling good classification of waxy and fluffy isolates. Our own choice of medium, stated above, undoubtedly aids differentiation of mycelial growth characteristics. Diurnal exposure to light, after the 7-day period in darkness, also enhances the fluffy-type morphology of aggressive isolates.

The identification of the aggressive and nonaggressive strains provides an opportunity for a new look at many of the questions posed by Dutch elm disease.

History of the Disease

Dutch elm disease was first described in Western Europe in 1918, and in Britain disease severity reached a peak between 1931 and 1937 and then declined. A high proportion of the elm population survived. In the Netherlands the disease was more destructive, but in recent years there has been little infection among the remaining elms. The disease was carried on elm logs imported for veneer to the United States about 1930, resulting in continuous heavy losses, and it has progressed across the Continent. With our present knowledge, the cultural descriptions of Bea Schwarz (*1922*) and Walter (*1937*) take on a new perspective. Bea Schwarz described the fungus as developing as "white filamentous mycelium which spread out from the wood in concentric rings by day and by night." She referred, by way of contrast, to some cultures that were sticky, with many yeast-like spores. Walter's description of the "typical isolate" (*Walter 1937*) corresponds closely with our fluffy type, and he also describes a number of other cultures, some with a yeast-like appearance.

It would thus seem that the aggressive and nonaggressive strains were originally present in both Europe and America. Since that time the aggressive strain has apparently declined within the *C. ulmi* population of northwest Europe, but not in North America. Thus Tchernoff (*1965*), in his description of cultural variation in Dutch isolates, described three basic cultural types, none of which bore any similarity to the aggressive strain. Re-importation of the aggressive strain on rock elm logs has now apparently led to a resurgence of the disease in Britain.

Population Dynamics and Ecology of C. ulmi

The ability to recognize the two strains in culture also brings into focus a previously unconsidered aspect of Dutch elm disease: the population dynamics of the pathogen. It enables sampling of the distribution and frequency of

aggressive and nonaggressive isolates to be carried out over a wide range of circumstances, from broad geographical regions down to local populations of elms, within individual trees, or even on the surface of a single beetle.

Most is known at present of the current situations in Britain and in the United States, and these are of particular interest as they appear to represent somewhat contrasting situations. In Britain we appear to be dealing with the interaction of the elements of two populations of the fungus hitherto geographically isolated: one aggressive, most probably originating from within the North American population; the other nonaggressive, representing the residual population of the fungus from the previous British epidemic, following its decline during the 1930s (*Brasier and Gibbs 1973*). Sampling on the basis of cultural characters has made possible a ready distinction between primary foci of the aggressive strain and local flare-ups of the nonaggressive strain, and has allowed the aggressive strain to be detected in advance of the main disease front. Results have also shown that both strains are present in the main disease areas, the aggressive strain predominant (*Gibbs and Brasier 1973*). It thus appears that the nonaggressive strain may benefit to some extent from the build-up of the aggressive strain. In current research at Alice Holt we are monitoring the relationship between the two strains in nature by taking annual samples from sites with a range of disease incidence. As both compatibility types of *C. ulmi* are present in the country, the possibility of the appearance of intermediate phenotypes resulting from outcrossing between the two strains is being investigated.

In the United States, samples have indicated that the aggressive strain is widespread. It appears that the continued presence of the aggressive strain is probably responsible for the maintained activity and spread of the disease in North America, although it should be noted that the nonaggressive

strain is also capable of causing severe disease on *Ulmus americana* (*Gibbs et al. 1972, Gibbs and Brasier 1973*).

Clearly many questions remain to be answered, particularly the reason for the apparent decline in the aggressive strain in Britain and other parts of Northwest Europe since the 1930s, and its maintained activity in North America. Our work may shed light on some of these questions, but many questions can be answered only by detailed information on the distribution of the strains in different parts of North America.

World-Wide Distribution of Strains

We need to learn more about the status of the two strains of the fungus throughout the world. A summary of our present knowledge is shown in table 1. In December 1972 we isolated the aggressive strain from elm twig material from the Friesland area of Holland (material sent by H. M. Heybroek). Later, we typed an isolate from Iran as the aggressive strain (isolate from H. S. McNabb), and during the past month (August 1973) we have isolated the aggressive strain from twig samples collected by McNabb in the Paris basin (France), Po valley (Italy), and near Freiburg (W. Germany).

Our investigations of the trade in rock elm have provided

Table 1.—Cultural characters of isolates of C. *ulmi* from Europe, North America, and Asia examined up to December 1972

[Based on growth rate and culture morphology]

Situation	Isolates	Fluffy	Waxy
France	5	0	5
Netherlands	10	1	9
Canada	4	4	0
U.S.A.	0	7	2
Iran	1	1	0

information that some rock elm logs originating in Canada have been transhipped from Britain to the Continent in recent years. The presence of the aggressive strain in Holland appears to be a recent phenomenon, and the outbreak in the Paris basin may also have occurred only in the last few years (*Pinon 1973; and Lanier, L., personal communication*). It is possible that the situations in Britain, the Continent of Europe, and Iran reflect the dissemination of the aggressive strain by man, via his transport systems.

Another part of the world for which knowledge of the nature of the fungus will be of great interest is the Far East, because some workers (*Heybroek 1967*) consider that the disease may well have originated in this area.

If the outcome of this work is the discovery that in certain countries only the nonaggressive strain of the fungus is present, there may be important consequences for disease control through the introduction of new quarantine regulations.

Genetic Control of Pathogenicity in C. ulmi

The recognition of two strains of C. *ulmi* with definable cultural characters provides a new opportunity for the study of genetic aspects of the disease. In particular, crosses between aggressive and nonaggressive isolates should lead us to an understanding of the genetic control of pathogenicity, of growth rate and culture morphology, and of compatibility type. This field of study is one of our special interests at Alice Holt, and it is being closely integrated with our studies on the population dynamics and ecology of C. *ulmi.* Initial results of crosses between the two strains indicate that cultural characters, growth rate, and pathogenicity are under polygenic control.

In considering genetic control of pathogenicity and cultural characters, the possibility of cytoplasmic determination should not be overlooked. In view of the ever-increasing reports of the occurrence of viruses in fungi (*Hollings and Stone 1971*), and especially of the reported role of cyto-

plasmic factors in the control of hypovirulence in *Endothia parasitica* (*Grente and Sauret 1969*), we are collaborating with M. Hollings and O. M. Stone in an investigation of the possibility of a viral infection in one or another of the two strains of *C. ulmi.*

Breeding for Disease Resistance

One unfortunate aspect of the belated recognition of the aggressive strain is that elm breeders have been uncertain of the relative pathogenicity of the *C. ulmi* isolates that they have been using in their work. Clearly as much variation in the fungus as possible should be used for testing procedures in breeding programs. This applies whether resistance is of a purely *horizontal* type (*sensu Van der plank, 1968*; cf. also general resistance) or if *vertical* resistance conditioned by major genes (cf. specific resistance) is also involved. It has been stressed by Heybroek (*1969, 1970*) that the safest form of resistance available to the tree breeder is horizontal resistance, primarily because it does not carry with it the high risk attendant on vertical resistance of being overcome by a new race of the pathogen during the useful life of the tree. Fortunately the work of Heybroek (*1962*) and Lester and Smalley (*1972 a b & c*) has provided strong evidence that host resistance to *C. ulmi* is largely horizontal and under polygenic control.

With the identification of aggressive and nonaggressive strains of the fungus we are now in a position to extend this work by inoculating the two strains into a range of host varieties of varying degrees of susceptibility. Evidence for horizontal resistance will be confirmed if both aggressive and nonaggressive isolates put the varieties in the same ranking order (*Van der Plank 1968*). By way of illustration, table 2 gives some interim data on just such an experiment carried out at Alice Holt this summer, in which a number of different elms that have previously exhibited a wide range of susceptibility were tested against aggressive and nonaggressive

Table 2.—Disease severity in various elm clones inoculated with aggressive and nonaggressive strains of *C. ulmi*

[Percentage crown symptoms after 4 weeks wilt]

Clone	Aggressive	Nonaggressive
U. pumila Chinkota	0	0
U. x *hollandica* N390	6	0
U. Japonica	38	11
U. pumila x *U. rubra* (Hamburg hybrid)	66	12
U. Americana Moline	100	70

Experiment conducted in collaboration with H. M. Heybroek and H. S. McNabb.

isolates. Although the plants were much more variable than is desirable for such work, it can been seen that at the time of scoring, both strains put the various elms in the same order. However, if an experiment were to demonstrate differential interactions in which the relative susceptibility of certain varieties to the two strains were reversed, this would be evidence for the additional involvement of vertical resistance.

In spite of the belated recognition of the aggressive strain, the likelihood is that results from such experiments will confirm the breeder's belief that resistance is largely horizontal and thus support the breeding principles adopted in the past. It is clear, however, that the release of new varieties must be undertaken with some caution until there is adequate evidence not only that no major genes for virulence are available to the fungus, but also that the release of such varieties would not result in directional selection towards a significant increase in the aggressiveness of the *C. ulmi* population.

Physiology of C. ulmi and the Host Parasite Relationship

Detailed comparative study of the differences in the morphological, physiological, and biochemical characteristics of the aggressive and nonaggressive strains *in vitro* may give some indication both of the physiological basis of pathogeni-

city and of the mechanisms of resistance. The ready growth of the fungus in liquid culture should facilitate analysis of differences in metabolic activity and the use of analytical techniques such as serological assay and isoenzyme studies. Similar studies of the two strains in the host are also required. From the pattern of disease development in the tree there is no doubt that the aggressive strain has a greater ability to invade the host than the nonaggressive. In addition to the differences in symptoms following inoculation, this is demonstrated in the frequency with which the aggressive strain has been observed to move outwards across the annual rings and cause disease recurrence in the year after infection (*Burdekin and Gibbs 1972*) and its ready spread through roots to adjacent healthy trees. Comparative study of the behavior of the two strains *in vivo*, including investigation of differences in enzyme and toxin production, rate and form of sporulation, induction of tyloses, and other host responses, may make a major contribution to the understanding of the etiology of the disease.

Significance for Short-Term Control Measures

Although perhaps the main significance of variation in the pathogen for disease control lies in its importance for breeding for resistance, there are also implications for short-term control measures aimed at the preservation of existing trees of high amenity value. Thus the success of measures such as pruning out of diseased branches, or the severing of root systems to prevent transfer of infection is likely to depend on the pathogenicity of the form of the fungus involved. This could well be particularly important on hosts such as *Ulmus americana* in which the nonaggressive strain can also cause severe symptoms but in which it may not move as quickly through the tree as the aggressive strain. Similar considerations could well apply to the therapeutic use of fungicide injection and other forms of chemical control.

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DISCUSSION

Chairman: H. M. Heybroek, Stichting Bosbouwproefstation, De Dorschkamp, Wageningen, Bosrandweg 20, Postbus 23, Holland.

McNabb: About 500 isolates of *C. ulmi* were collected in Ames, Iowa, this summer; and all but 2 or 3 were of the aggressive form described by Clive Brasier. We used the same technique that he used in determining these characteristics. In the area of Paris, France, Northern Italy, and Southwestern Germany there appear to be both aggressive and nonaggressive isolates present, according to tests carried out by Brasier with isolates collected by my Scouts and me this past summer.

Schreiber: We initiated a study, to determine if pathogenic variability occurred in isolates of *Ceratocystis ulmi* and might explain, in part, observed differences in severity of Dutch elm disease in the Northeastern and Midwestern United States.

Isolates were selected for testing from widely diverse areas throughout the continental U.S. The fungus was grown from wood from diseased trees to circumvent any effects on pathogenicity of carrying the isolates in culture. Standard spore suspensions of the isolates were inoculated into the lower trunk of *Ulmus americana* and *U. pumila* trees. The isolates produced significant differences in foliar symptoms in the same order of magnitude on both tree species. Most isolates were aggressive, one was intermediate and a few were only mildly pathogenic.

Three of the most aggressive and the three least aggressive isolates were re-isolated from both elm species. All were isolated with about equal frequency from American elm but the more aggressive ones were recovered with significantly greater frequency than the less aggressive isolates from Siberian elm.

Pathogenicity was correlated with the cultural characteristics of growth rate, mycelial habit on potato dextrose (PDA) and malt extract (MEA) agar and coremial production on wood discs from branches of American and Siberian elms. The less aggressive isolates grew more slowly on both PDA and MEA than did the aggressive ones, although several aggressive isolates also grew slowly. Mycelium of all isolates grew appressed to the MEA. On PDA, the most aggressive isolates were intermediate between appressed and aerial; The least aggressive isolates, with the exception of one aerial type, were more appressed. Finally, the least aggressive isolates produced few or no coremia on wood discs of both species. The most aggressive isolates, with one exception, produced the most coremia on discs of both species.

Chairman: When the aggressive strain was first discovered, we wondered where it came from and worried what it was going to do to our European elm populations and to the breeding programs for elm. Later we realized that at least from a scientific standpoint the weak strain is more remarkable. It seems to be able to survive side by side with the aggres-

sive strain in parts of the USA, and it apparently managed to replace more aggressive strains in northwestern Europe around 1940. There is apparently some form of a balance possible between the two types.

It seems most important to me for us to study and understand the balance between the two strains. It might allow us to predict the course of the current epidemic and even to manipulate it. It is not unique that a weaker strain of a parasite should win out over a more aggressive type, the well-known example being myxomatosis. The first known strains of this virus were highly aggressive, killing rabbits rapidly. The virus thereby tended to be self-destructive, as the infected rabbits lived so short a time that they had little opportunity to infect others. Soon a less aggressive strain took over, killing more slowly and thereby allowing the victim more time to infect other animals. Considering its entire life-cycle, the less aggressive strain appeared to have the higher fitness.

In the question about the mechanism of a balance between the two strains of *Ceratocystis ulmi*, I visualize two possible answers. The first has to do with the fact that *C. ulmi* is not an obligate parasite. It has a long saprophytic phase, in which it lives in and on the beetle, grows in the galleries of the beetle, and produces coremiospores or other slimy spores that will stick to the young beetle when it hatches. It does not seem necessary for the survival of the fungus for it to kill elms: it seems able to survive and complete its cycle just on beetles and in their galleries. Maybe this is what it did in Britain up to 1967, just causing some slight disease-symptoms in an elm here and there as a by-product. It could be hypothesized that during such a prolonged saprophytic stage the fungus would tend to lose its virulence just as it does when we keep it in culture for years instead of inoculating it into elms every now and then. It is also conceivable that when both a more aggressive and a less aggressive strain are present, the latter may have an advantage over the former, in being better adapted to this type of life: for example by surviving better in the galleries or by producing sufficient slimy spores under conditions when no coremia can be found. This then could lead to a slow elimination of the aggressive strain if only this advantage could more than offset the advantage of an aggressive strain in that it can kill trees more effectively.

For the fungus, survival lies above all in riding on a beetle or growing in a beetle's gallery. No matter how successful the fungus is in killing a tree, its parasitic phase in the interior of a tree is a blind alley for the fungus unless it is picked up again at some phase by a beetle. How often will an uninfected beetle or its larval offspring pick up the fungus that killed the tree in which it breeds?

Even if the weak strain was far stronger than the aggressive one in the competition during the saprophytic phase of the fungus, there would still be a possibility open for an escape, for an outbreak of the aggressive type: not the entire offspring of a fungus-carrying mother-beetle needs to be infected, so that some part of the beetle population can be free of the fungus. If some of these would pick up the aggressive strain, they could start a completely new and independent epidemic, killing a great many elms before the weak strain would regain the upper hand.

Such thoughts primarily highlight our lack of knowledge about the interplay between beetle and fungus, about the way the fungus moves through the beetle population. We know little about that beyond the fact that the fungus normally is passed on as a congeneric contamination in the maternal line, and perhaps as a venereal contamination at mating. We do not know to what extent uninfected beetles that carry out their maturation-feeding on infected elms will pick up the fungus, and to what extent uninfected beetles that breed in an elm log containing the fungus in its outer rings will have infected offspring. Some of these problems can be solved by rather simple experimentation, but they certainly require a very close cooperation between entomologist and mycologist.

The second possible answer to the question, why this nonaggressive strain can survive so well, has been mentioned already. When considering the slower growth on several media, the lower pathogenicity and the apparently reduced capacity for producing coremia, as observed in the nonaggressive strain, one may wonder whether it perhaps has some viral or other disease. If such a diseased condition were to some degree contagious, it could explain why the healthy strains might become a minority or even extinct under certain conditions.

Summarizing, there is a fascinating problem in the weak strain, in how it manages to survive in competition and possibly even win out over the aggressive one.

Van Alfen: Grente observed the gradual decline of chestnut blight from a chestnut plantation in France. It was found that this decline was due to a hypovirulent strain of the pathogen *Endothia parasitica*. When one co-inoculates a chestnut tree with a virulent and a hypovirulent strain of the fungus, a small canker typical of that caused by the hypovirulent strain alone appears. The hypovirulent strain can also pass its hypovirulence to a virulent strain in culture by hyphal anastomosis.

One explanation for such behavior is that the hypovirulent strain contains a virus. The behavior of the aggressive and nonaggressive strains of *C. ulmi* appears to be much different from the *Endothia* strains. It would be surprising if the difference in the *C. ulmi* strains was due to the presence of a virus in one strain and not the other.

Last: Will the aggressive and nonaggressive strains of *C. ulmi* anastomose? Could they do so within the infected tree? If this occurred would this possibly slow the aggressive strain?

Brasier: No one has looked at the possibility of hyphal anastomoses in cultures of *C. ulmi* so far as I know.

We have considered the possibility of virus infection in the nonaggressive strain and cytoplasmic particles might be transferred to the cytoplasm of aggressive isolates by anastomosis, as in *Endothia*. So far our searches for a virus have been negative.

Another possibility, of course, is anastomosis leading to heterokaryon formation but we know nothing of this at present.

Smalley: It is possible to derive nonaggressive isolates from virulent cultures. These are isolates cultured from old cultures. If these derived nonaggressive isolates are inoculated into *U. americana*, the trees will die uniformly.

Holmes: Working with mono-ascospore cultures derived from crosses I made in the Netherlands in 1962 and 1963, between fresh Dutch and U.S. isolates, I found cultures that were very variable in appearance when grown on cherry agar. Single-ascospore isolates produced cultures that varied in cultural characteristics from fluffy to powdery to waxy, from very white to cream-colored, and with or without concentric, day-night zonations, as described by Brasier, and also from very high to very low virulence, but we could not find a relation between virulence and any other character that we recorded.

Ouellette: We have been working with a fluffy isolate. If this isolate is inoculated into Siberian elm it is possible to get waxy isolates from these inoculated trees.

Brasier: Do you have any evidence what kind of selection pressure is going on within the tree?

Ouellette: No.

Brasier: In southern Great Britain there appears to have been a selection pressure against aggressiveness in the 1930s, whereas in North America this does not appear to be the case.

Holmes: I'm sure that the aggressive strain has been present in England in the past because the losses there were said to be heavier in the 1930s than in the 1940s and 1950s. Considering differences found in the U.S.A., probably both strains occurred there, too, all along. That is, both strains have occurred on both continents. And both still occur on both continents.

Hubbes: Still nonaggressive strains will kill American elm.

Brasier: Yet according to Van der Plank, the aggressive strain might be expected to decline in a population of host plants that are as susceptible as American elm.

Holmes: Exactly so, and therefore, how do you account for the situation in the U.K., where the elm population is *more* resistant than *Ulmus americana*, and therefore a *more* aggressive strain should have an advantage, instead of a *less* aggressive strain having an advantage!

Brasier: This point was stressed in my presentation. Clearly we need more information. The aggressive strain probably does have more aggressiveness than is required for it to come into better equilibrium with English elm. The nonaggressive strain would appear to be in better harmony with our English elm population, causing only minor flare-ups of disease from time to time.

We must also remember the importance of the beetle in this situation and the selective effect it may exert upon the fungus (both saprophytic and parasitic stages). It may take some time for selection pressures to exert any measurable effect following the introduction of the aggressive strain of *C. ulmi* into the U.K.

McNabb: There may also be some differences in the numbers of perithecia found in North America and in the U.K. Perithecia are very common in the Netherlands and possibly they have not been looked for intensively enough in this country. It also seems to me that it should be possible to have both aggressive and nonaggressive strains in the same tree.

Smalley: The beetle may be very significant in this story. This is because of the oily secretion on their bodies that may have some influence on spore adherence.

Gardiner: Have you had any evidence that *Hylurgopinus rufipes* has become established around the ports of entry in the U.K.?

Brasier: No, we have not had any evidence.

Gardiner: If they did become established, they would probably mostly overwinter as adults. In Canada, we have found that a high percentage of overwintering *H. rufipes* adults carry *C. ulmi* spores, but relatively fewer of the overwintering larval group.

Brasier: In contrast, in the United Kingdom, overwintering beetles appear to be uncommon, overwintering larvae are the rule. We also have another beetle in addition to *Scolytus multistriatus*. This beetle is *Scolytus scolytus*, which is much bigger, produces much larger feeding wounds, and may carry more spores.

Chairman: Up to now we discussed the variability of the fungus. Let us now consider how the (re?) appearance of the aggressive strain in Europe affects the breeding programs, apart from giving nightmares to the breeders.

For the U.S. breeding programs, little seems to be changed. For the European program, however, a complete reorientation is needed. Our Commelin elm appears to be susceptible to the new strain, which is discomforting when considering that over 500,000 Commelin elms have been planted in our country. Even the Groeneveld elm is more or less susceptible.

Still, even more important is the question whether this is to happen again, whether clones of elm resistant to this "new" strain will eventually succumb to further unknown strains. Personally, I think that is unlikely to happen. We generally recognize on the one hand the *vertical* or *differential* type of resistance, which is often broken down by some new strain of the parasite, on the other hand the *horizontal* or *uniform* type of resistance, which is regarded as durable.

The resistance we know is clearly not a typical case of *vertical* resistance. Though Francis Holmes as well as Tchernoff did find a certain interaction between strains and clones as far as disease expression is concerned, the use of different strains does not lead to the dramatic reversals in the order of susceptibility of clones as associated with vertical resistance.

From available data, the impression is gained of a *horizontal* resistance:

1. In broad outlines the relative resistance of clones is maintained.
2. Resistance is clearly polygenic. In the Dutch breeding-program, there was a slow build-up of resistance in the course of several generations.
3. Resistance is not based on a very specific hypersensitivity reaction but mainly on a general anatomical character of the host, that is on the size and grouping of the vessels; and perhaps to some extent on a more rapid formation of tyloses.

One thing does not fit in the picture. Differences in aggressiveness are generally understood to be based on a polygenic system in the parasite so that many genes add up to cause a slight increase in aggressiveness.

Theoretically, one would therefore expect to find a monomodal frequency distribution; in reality, however, we seem to find some bimodal distribution in which intermediate aggressiveness is under represented.

In Europe, this might be explained by the newness of the aggressive strain; if the same occurred in N. America, it would be much more difficult to explain.

Zadoks (in "Biology of rust resistance in trees," U.S. Forest Serv. Misc. Publ. 1221, 1972, 43-62) has suggested that horizontal and vertical resistance may be just the extremes of a range, implying that there are intermediate cases to be found. Perhaps this concept could be further developed for a situation as we have in DED, where an entire genus with a wide variation in genetic make-up is concerned.

I would not be surprised to find a certain "specific" resistance to the new strain in Asiatic species—we have perhaps some preliminary evidence for that.

So for further breeding I would recommend four things:

1. Continue in the same direction as before, combining resistance from many different sources.
2. Further analyze the basis of resistance.
3. Try to use tolerance where available (the extreme example being *Hemiptelea*).
4. Test Asiatic species and explore their variability on a larger scale.

Townsend: Larry Schreiber and I have studied the possibility of interactions occurring between different *C. ulmi* isolates and different *Ulmus* genotypes. We have inoculated seedlings of *U. americana, U. pumila, U. carpinifolia*, and *U. glabra* with a range of aggressive and nonaggressive isolates. Also we have inoculated full-sib hybrid seedlings of diverse parentage, again using the same isolates.

Our studies to date indicate no significant interaction between isolates of *C. ulmi* and different host materials of *Ulmus*. That is, an aggressive isolate can be expected to cause greater symptom development than a nonaggressive isolate, regardless of the gentic make-up of the *Ulmus* host. These kinds of studies will be expanded in the future to include the use of clonal material. Results to date indicate that resistant, full-sib, hybrid seedlings show good horizontal resistance to a broad spectrum of isolates.

Elgersma: We have shown that tyloses form more rapidly in NL 390, resistant to Dutch elm disease, than the susceptible *U. hollandica* 'Belgica'. Rapid tylose formation thus may be a resistance mechanism. (See Elgersma, D.M., 1973. Neth. J. Plant Pathol. 79:218-220.)

Sinclair: A similar kind of resistance seems to be present in a minor proportion of native *Ulmus americana*. Far fewer fungal propagules can be obtained from them than from the susceptible trees, if isolated at fixed intervals after artificial inoculation of branches. Disease symptoms are more localized, too.

Ouellette: Siberian elm is resistant and produces tyloses when inoculated. When tyloses are formed, the S3 layer is pushed into the vessel, and the fungus can penetrate this layer. Therefore the presence of tyloses probably is not enough to impart resistance in Siberian elm. Therefore the more rapid production of tyloses in the resistant trees may not give the best correlation to resistance.

Campana: I did a study 2 years ago on the spore movement in inoculated *U. americana* and *U. pumila*. The spores moved much slower in *U. pumila* and I could not re-isolate the fungus from these trees.

In our irradiation work, we have shown that irradiation changes the anatomy of the wood, causing smaller vessels to be produced, which seems to be related to the resistance of these trees.

Hubbes: However you must remember that *C. ulmi* has spores of several different sizes. When considering these changes in vessel size, one must also remember the sizes of the spores.

Lester: We have used a different approach to breeding for resistance to Dutch elm disease.

1. We selected for resistance in *U. americana*. But due to problems with propagation, tetraploid problems, and to the fact that root-cuttings from selected "resistant" trees turned out to be susceptible, we have stopped looking for resistance in American elm.
2. Instead we are working with *U. japonica* crossed with *U. pumila* and *U. rubra*. We have developed an hypothesis about the percentages of *U. japonica*, *U. pumila* and *U. rubra* that will give us resistance as well as a desirable tree. The percentages that appear to be the best are: 30-50 percent pumila; 30-70 percent japonica; and 10 percent rubra.
3. Our goal is to produce seedling populations of good growth and sufficient homogeneity in which at least 90 percent of the individuals are resistant to DED. The realization of this goal seems to be close. (See D. T. Lester and E. B. Smalley, 1972.
   Improvement to elms through interspecific hybridzation with Asian species. IUFRO genetics—Sabrao and joint symposia, Tokyo 1972. C-5 (V) 1-10).

Schreiber: In our program on selection and testing of elms for shade tree use we used the collection of elms with highly varied phenotypes and genotypes that has been assembled at the Agricultural Research Service Shade Tree and Ornamental Plants Laboratory at Delaware, Ohio. For the last 7 years we have been engaged in an intensive program of evaluation of these plants based on pest resistance and horticultural desirability for shade tree and ornamental use.

At present, following preliminary screening, eight trees, including two American elms, four *U. carpinifolias* and two selections of *U. wilsoniana*, have qualified for further testing. Advanced testing includes large scale vegetative propagation and distribution of ramets to selected test sites for studies of their environmental adaptability as well as disease resistance. In addition, observations of growth habit and disease resistance are made throughout several growing seasons at our laboratory.

Figure 2.—A resistant elm clone, N148 x *U. pumila.*

To date, our most promising selection is a clone derived from a cross between Siberian elm, *Ulmus pumila*, and a Netherlands selection, N148 (*U. hollandica* Vegeta x *U. carpinifolia* (fig. 2)). The tree has profuse upright branching and the dense foliage produces a compact crown. The leaves are dark green and smooth and the tree stands out in the fall because it retains its foliage and dark green color longer than other trees in the area. It is recommended for hardiness below zone three. A final release of this selection is expected following observation made during the 1974 growing season.

Townsend: Our breeding work over the past 3 years has involved the creation of many different hybrids from a wide variety (in species, size, shape, disease resistance) of parent trees. For example, we have crossed several of Dr. Larry Schreiber's selctions with each other, and also with some of the Netherland's selections. The following new crosses (heretofore unreported) were successfully made and verified in 1971 and 1972: *U. carpinifolia* x *U. parvifolia*; *U. carpinifolia* x *U. rubra*; *U. glabra x U. rubra*; *U. pumila x U. parvifolia*; *U. rubra* x *U. glabra*; and *U. rubra* x *U. carpinifolia*. The 1970 hybrids were inoculated this year (1973). When used as male parents, N282 and N339 transmit higher doses of resistance than (N274 x N215). We have found considerable variation in symptom development caused by differences among sites. When *U. pumila* is used as a female parent, most hybrid progenies exhibit some initial foliar symptoms but by the end of the season they have recovered fully, with little or no central leader dieback.

We hope to be able to release (as clones) some of the new hybrids according to the following schedule:

Year No.	*Action to Take*
1	Inoculate progenies (3-year-old).
2	Propagate most promising clones (most resistance; horticultural desirability; growth; etc.).
3 & 4	Run seasonal susceptibility trials on ramets.
5	Second selection based on seasonal susceptibility test results.
6	Ship best clones to outplanting sites for testing.
7 & 8	Inoculate clonal material located at testing sites.
9	Release superior clones.

The above program takes into account and measures effects from variation in the planting environment, pathogen, and host. By no means will it preclude the development of superior F_2 stock.

SANITATION AND DUTCH ELM DISEASE CONTROL

by DAN NEELY, *plant pathologist, Illinois Natural History Survey, Urbana, Illinois, U.S.A.*

THIS IS an opening statement on sanitation as it relates to control of the Dutch elm disease (DED). It is intended to accomplish what the introduction and review of literature do in a scientific paper. The materials and methods, results, and conclusions on experiences or experiments related to sanitation are to be provided by those of you contributing to the following discussion. My objectives are to define sanitation, briefly describe some experimental studies upon which sanitation practices are based, discuss the practical application of these research results, demonstrate the need for additional information, and stimulate a discussion from those of you present who can contribute to our understanding of the subject.

Sanitation is defined as the use of measures to preserve or restore health, to free the environs of agents injurious to health. Felt (*1933*) used the term *tree sanitation* to describe clean-up procedures beneficial in preserving elms from the DED. The term sanitation is now widely used in describing plant disease control measures.

I am indebted to Stevens (*1933*), Readio (*1935*), and Clinton and McCormick (*1936*), for reviewing the early history of the DED in Europe. Scientists in the Netherlands identified *Ceratocystis ulmi* (Buisman) C. Moreau as the fungal agent causing the disease. The first paper definitely

referring to the disease (*Spierenburg 1921*) mentioned the fact that *Scolytus scolytus* Fabricius, the larger European elm bark beetle, was found on many diseased trees as a secondary attacker. Some researchers at the time considered the beetles to be the primary cause of the dying of elms.

Before discovery of DED in North America, the Europeans had established to their satisfaction that insects were indeed the vectors of the causal fungus with the following associations: (1) the bark beetles (*S. scolytus* and *S. multistriatus*) are attracted to diseased trees in which they lay eggs. (2) Coremia of *C. ulmi* are present in pupal cells and maternal galleries. (3) Viable spores of *C. ulmi* are carried both internally and externally by emerging adult beetles. (4) During maturation beetles feed on twigs of healthy elms and inoculate the trees.

Before 1935, control of DED in Europe was tried by removal and disposal of infected trees to prevent beetle emergence and flight, and by breeding of resident elms. Before the advent of DDT, spraying healthy elms with an insecticide was considered ineffective (*Fransen 1939a*). In the Netherlands, although control efforts (removal and disposal) were compulsory, *Ulmus hollandica* died at the annual rate of 1 to 6 percent of the residual elm population from 1930 through 1943 (*Went 1954*). In Germany, no federal laws were enacted, but some states imposed fines or imprisonment as punishment for failure to follow sanitation procedures. No DED control efforts were enforced in France, Belgium, or Italy. Within 1 year after the discovery of the disease in England, it was decided that eradication was impossible, and the disease ran an uninterrupted course for many years. Because sanitation procedures were not carried out, or even required, in all countries, many elm stands in Europe disappeared in the 1920s and 1930s.

Immediately after the 1930 discovery of DED in the United States, an attempt was made to eradicate the disease (*White 1935*, *Worthley 1936*, *Brewer 1941*). The prompt

removal of a few trees might have prevented a rapid increase of the disease in Ohio, but in 1932 DED was found in several locations in three additional states along the Atlantic coast. Effective January 1, 1935, a quarantine prohibited the importation into this country of elm veneer logs, the apparent source of *C. ulmi.* Of the 14 areas exposed to *C. ulmi* by veneer-log imports, elms in 6 were found to be contaminated by DED. From 1935 through 1940 the federal and state governments spent $24,000,000 on control efforts, 80 percent of the money coming from emergency relief funds during the depression years.

These efforts succeeded in limiting the number of trees infected, but not in limiting the size of the area affected. The program was based on thorough scouting, sampling of suspected trees, laboratory isolation of *C. ulmi,* and tree destruction (*True and Slowata 1939*). By 1940 fewer than 1 in 8,000 elms in the region of infection had succumbed to the disease. This fine record was ascribed to the sanitation program (the removal of all dead and dying elms in cities and woodlots throughout the region of infection). Political considerations concerning financing and the quality of the men employed handicapped the control efforts. With full employment during World War II and discontinuance of federal emergency funding, the program died (*Brewer 1943*).

Soon after the 1944 discovery of DED in Quebec, Canada also attempted eradication (*Pomerleau 1961*). The work was abandoned in 1950, when it was realized that the fungus was too firmly and extensively established in the Province. In the following 4 years the incidence of DED increased.

No one has yet succeeded in permanently eradicating the DED from a susceptible elm population, but the eradication programs have proved that sanitation procedures will limit disease occurrence.

Due to criticism of the eradication program and the desire for more effective control procedures, American scientists began an intensive study of DED. Smucker (*1937*) found

that *C. ulmi* would not invade elms unless injuries through the bark were present. Because the primary injuring agent of elms is the elm bark beetles, *S. multistriatus* and *Hylurgopinus rufipes* Eichh., the native elm bark beetle, cooperation between plant pathologists and entomologists became imperative.

Entomologists worked to confirm the studies of Fransen and his co-workers (1931, 1935, 1939a) which proved that *C. ulmi* was transmitted by elm bark beetles. The association with *C. ulmi* changed our opinion of *S. multistriatus*: an insect of no economic importance became one of prime importance (*Felt 1935*). In much of the United States, *S. multistriatus* has two broods per year, with one peak emergence in June and another in August. The adults find DED-affected wood well suited for colonizing and reproducing in enormous numbers. The recently emerged adults feed in elm twig crotches near the emergence site and in the vicinity of wood attractive as breeding sites. All elm species are palatable to *S. multistriatus (Felt 1934, Collins 1938b, Fransen 1939b, Wallace 1940)*.

Chapman (*1910*) first found *S. multistriatus* in America in 1909; *H. rufipes* has long been known here. *H. rufipes* feeds on the bark of the trunk and branches and not the bark of twigs (*Collins 1938a, Kaston and Riggs 1938, Pomerleau 1965a, Thompson and Matthysse 1972)*. *H. rufipes* seldom penetrates into wood tissue in its feeding activities.

Convincing proof that elm bark beetles are vectors of *C. ulmi* did not come easily. Middleton et al. (*1935*) and Collins et al. (*1936*), transferred beetles that emerged from infected trees to healthy trees. Later isolation of the fungus from once healthy elm tissue proved that transmission of *C. ulmi* had occurred. The infected trees failed to show typical disease symptoms. Parker et al. (*1941*) transmitted *C. ulmi* through *S. multistriatus*, and the elms subsequently developed DED infection symptoms. It was apparent that large numbers of elm bark beetles and large numbers of beetle-feeding scars

were necessary in experiments routinely to transmit *C. ulmi* and to inoculate and infect elm trees. Wolfenbarger (*1945*) measured American elms, *U. americana*, and determined the area of bark suitable for beetle reproduction and the number of twig crotches available for beetle feeding.

In the search for beetle-feeding scars it became evident that not all dead elm material was suitable for beetle reproduction. Often there were no feeding wounds in elm trees having large dry branches. Feeding scars were evident only near elm wood where young adult beetles emerged or near wood attractive to adults seeking brood wood (*Collins 1938b*). Elm material suitable for bark beetle reproduction is probably the most important single factor in the maintenance and spread of the DED pathogen (*Connola et al. 1947*). It must be freshly cut, recently killed, or suddenly weakened elm trees or parts of trees (*Welch 1953*). Although S. *multistriatus* will attack branches as small as ½ inch in diameter, 92 percent of the beetle population is found in elm material larger than 3 inches in diameter and 99 percent in material larger than 2 inches. Limbs dead 1 to several months are not infested by S. *multistriatus (Baker 1941)*.

The distance bark beetles fly in feeding and breeding activities determines the rate of spread of the disease and the extent of sanitation required to clean a local area. Wolfenbarger and Jones (*1943*) found crotch injuries mostly less than 150 feet from emergence sites and within 50 feet of suitable breeding sites. Brood galleries were found up to 4 miles from the point of emergence, although most were less than 4,000 feet from the point of emergence. Injuries decreased as distance from the point of emergence increased. Zentmyer et al. (*1944*) found that 75 percent of all new infections were within 100 feet of a source of inoculum and that 40 percent of the trees within 75 feet of the inoculum source became infected. The maximum distance spread in three plots was 180 feet. A regression curve showed little like-

lihood of any infections beyond 1,000 feet. Parker et al. (*1947*) found 60 percent of new infections within 100 feet of the source, 80 percent within 250 feet, and none more than 500 feet. The movement of beetles from points of emergence is relatively restricted. Because of the short distances the beetles travel, it should be possible with sanitation procedures to control DED in urban areas. Long-distance dissemination of bark beetles can occur by air currents (*Felt 1937*) and transportation conveyances (*Hafstad 1958*).

The percentage of beetles transmitting *C. ulmi* will affect the intensity of disease in the area. Collins et al. (*1940*) and Rankin et al. (*1941*), in field studies, found 0.9 percent to 15 percent of *S. multistriatus* carrying the fungus to elm trap logs. Parker et al. (*1947*) found that 1.4 to 42 percent of the beetles emerging from elms were contaminated. All found that elm material free of DED could be a source of *C. ulmi*-infested emerging beetles. *C. ulmi* carried into brood galleries proliferates profusely and contaminates the next generation of beetles. Male beetles may also disseminate *C. ulmi* in mating activities (*Hoffman 1940*). *C. ulmi* has even been identified in beetle galleries in areas where DED has not been found.

Trap logs seemed to offer an accessory means of reducing the beetle population in an area. Martin (*1936*) found little significant difference in the amount of infestation in freshly cut logs due to placement site or moisture content. Whitten and Baker (*1939*) found that felled trees are more attractive to beetles than are girdled trees, chemically killed trees, or elm logs, and that treatment with sodium chlorate made felled trees even more attractive to beetles.

C. ulmi survives as a saprophyte. Plant pathologists have studied its existence apart from its insect and pathological associations. Smucker (*1935*) found that air currents can carry *C. ulmi* spores 5 to 40 feet with resulting infections of elms. True and Slowata (*1940*) isolated *C. ulmi* readily from woodpiles 4 months after the wood had been cut, but infre-

quently 20 months after cutting. After isolating from 2-year-old stumps of elm, Graham (*1936*) recovered *C. ulmi* from 23 percent of the living stumps and 4 percent of the dead stumps. He used copper sulfate to kill stumps and reduce the inoculum potential in the area. Tyler and Parker (*1945*) studied the temperature and moisture requirements of *C. ulmi*. They found that the fungus will not persist in elm wood that is dried rapidly.

The period of susceptibility of elms to infection is the period when sanitation procedures should have the area free of insect vectors of the disease. June, July, and August inoculations are most likely to result in systemic infections of elms (*Pomerleau 1965b, Smalley and Kais 1966, Neely 1968*).

In many elms, DED infections become localized, and the entire tree is not killed. Many elms recover from the disease (*Smucker 1940, Banfield 1968*). One factor contributing to apparent recovery is the resistance of the particular *Ulmus* species to the strain or strains of *C. ulmi* in the area (*Neely and Carter 1965*). For many years, in England, recovery from DED was commonplace, and the sanitation procedures called for removal only of badly diseased English elms (*Peace 1960*). In the United States, once major branches of the American elm have developed disease symptoms, attempts to control the disease by pruning have had only limited success (*May and Douglas 1944, Hart 1970*). Sanitation procedures call for complete removal and destruction of all trees known to have the DED.

Elm material suitable for bark beetle breeding must be destroyed before beetle emergence. The short beetle generation time (5 to 7 weeks) requires prompt action. Burning is the most reliable method for rendering wood entirely safe. Burying can be satisfactory. Heat treatments by fire, steam, or hot water rarely are feasible (*Connola et al. 1947*). Stripping the bark from the wood will prevent beetle attack. Spraying with DDT [or methoxychlor] also has been satis-

factory (*Whitten 1955*). Bark beetles survive the chipping of infested elm material.

An additional procedure to supplement destruction of elm wood is the use of chemical repellents to prevent bark beetle colonization in disease trees (*Craighead and St. George 1938, Whitten 1941, Himelick and Neely 1961*). Potassium iodide placed in ax frills is an effective and safe substitute for sodium arsenite for this purpose (*Himelick and Neely 1963*).

Individuals in different states and nations have compiled these research results into recommendations for control of DED. They vary greatly. Control is usually based on (1) sanitation, (2) spraying, (3) root-graft control. A comprehensive set of recommendations was prepared by the Midwestern Chapter, International Shade Tree Conference (*Int. Shade Tree Conf. 1956*), titled *Guide for Community-Wide Control of Dutch Elm Disease.*

Each phase of the control procedures has advantages and disadvantages. The advantages, procedures, and priorities for sanitation practices were presented by Campana (*1956*). The reasons sanitation often fails were discussed by Whitten (*1956*).

Unfortunately, no field studies have been designed properly to compare sanitation alone and spraying alone or sanitation alone with sanitation and spraying. Observations of municipal control efforts provide the best information available. Matthysse (*1958*) stated that DDT spraying reduced losses to DED in a sanitation area only an additional 37 percent. Whitten (*1955*) reported that sanitation in Princeton, New Jersey, reduced DED losses by 34 percent and that DDT spraying reduced losses by 90 percent. Neely (*1961*) found that losses on private property in Illinois cities (sanitation only) were somewhat higher than losses along streets (sanitation and spraying) and that both were much lower than losses in cities where neither control measure was practiced. Zentmyer et al. (*1946*) criticized the results of the eradication program in Connecticut, but Marsden (*1953*) used the

same data as an argument for sanitation. Losses were maintained at less than 1 percent of the elm population during the 7 years of control; but within 4 years after control ceased, losses were 4.2 percent. Miller et al. (*1969*) reported the results of control by sanitation in Syracuse, New York. During 14 years when sanitation procedures were implemented intensively, losses were held at a low level. During the next 6 years, when sanitation was no longer adequate, losses soared.

Research on DED has shown that proper sanitation for disease control usually involves an area larger than one-man controls. DED control, therefore, becomes a community problem. In community actions there are always the problems of: Who pays? How much? What legislation or ordinances are required to enforce compliance? What organization is responsible? Iowa State University prepared excellent material to assist communities with these decisions (*Riley et al. 1966*).

More than 50 cities in Illinois began comprehensive disease control programs soon after DED was found in the state. Many discontinued the programs. The reasons for failure were political, not scientific (*Van Camp 1960*). Twenty-six cities have maintained effective control programs for 17 years. Some communities recently discontinued spraying when restrictions were placed on the use of DDT, but have continued sanitation. Only with time will we know the results of this change (*Neely 1967 and 1972*).

The sanitation and spraying control procedures now recommended will limit DED infections if scrupulously followed, but they fully satisfy no one. Too few communities follow them. We need better DED control recommendations. I expect scientists in this room to provide them.

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DISCUSSION

Chairman: D. A. Burdekin, Forestry Commission Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, England.

Entomological Aspects of Sanitation

Lanier: The flight range of bark beetles is often underestimated. The range is influenced by many factors, including the presence of hosts at intermediate ranges, air currents, and odor trails. Beetles may perhaps have an effective range of up to 10 miles.

Smalley: Do the beetles have a specific time for flying and for attacking trees?

Lanier: Yes. The peak emergence time is between 1100 hrs and 1300 hrs, and the peak attack time is in the evenings at about sunset. The beetles have a natural diurnal rhythm that tells them when to emerge. During late afternoons there is greater air turbulence, which settles during the late evening, thus making odor trails easier to follow.

McNabb: Beetle flight is not as important as beetles hitchhiking on various forms of transport—railroads, highways, ships.

Thomas: Contests the idea that *Hylurgopinus rufipes* is not an efficient vector of DED, For a long time *H. rufipes* was the only vector in Canada and is still the only vector in Northern Ontario (Canada), where DED is present.

Worf: It was stated earlier that *H. rufipes* can overwinter as a larva and as an adult and that it carries larger numbers of spores. What kind of sanitation program can be used in an area where *H. rufipes* is the more important vector?

Gardiner: Central Ontario is the frontier of DED in Ontario, and in this area 1 generation per year seems to be the general rule, unlike farther south where 1½ generations occur. In our region, the population is fairly distinctly divided into 2 groups: one that overwinters as adults and the other as larvae. Overwintering adults emerge in early spring, feed in the crowns and then begin to produce their brood. The progeny emerge in August and September, and most of them appear to go into hibernation, although early emergers may start another brood. Overwintering larvae emerge in July; their progeny overwinter again as larvae. The present practice of removing diseased trees during the winter removes overwintering larvae but not overwintering adults. It also removes breeding material. The city of Sault Ste. Marie has an active removal program, and broods do not build up in the city. However, populations do build up outside the city, where sanitation is not practiced; and these beetles can infect city trees.

Worf: What about areas with overlapping ½ generation and with trees where the adults have left their galleries?

Gardiner: The areas with $1\frac{1}{2}$ generations per year present a similar situation as with 1 generation per year in respect to sanitation except that, as reported recently in New York State, you may have overwintering adults 1 year and overwintering larvae the next. The fact is, where a sanitation program is continuous, there is no build-up of suitable breeding material. When infected trees are detected during the summer survey and marked for removal, they are not suitable for *H. rufipes*. They would only be suitable the following year, except that they will have been removed, of course.

Wester: In some of my research conducted years ago in the Dutch elm disease laboratory of the USDA, I demonstrated that coremia development of *C. ulmi* in pupal chambers of *scolytus* was very important in disease transmission. Diseased logs racked 6 inches above the ground under woodland conditions were highly favorable for coremia production in beetle pupal chambers, while similar logs stores under moist sphagnum moss failed to produce any coremia in similar locations. Very high disease transmission was obtained by beetles from pupal chambers producing coremia from air-dry stored logs as opposed to no transmission with beetles from wet-stored logs not producing coremia in pupal chambers. Transmission was recognized by recovery of *C. ulmi* from beetle feeding wounds, which, however, did not result in infections, apparently because this was attempted under unfavorable late-summer conditions.

Neely: The municipal control programs in Illinois were based on Campana's work, which was done while he was employed there. When control was first initiated, there were 55 municipalities with control programs, of which 27 presently use sanitation alone or in conjunction with spraying. In 1957 to 1967, most of these municipalities sprayed and practiced sanitation measures with a goal to keep losses below 2 percent per year. Between 1957 and 1971 these communities experienced a loss of between 10 and 37 percent of the original elm population, while neighboring areas without any control programs had a loss of between 95 and 99 percent.

Conclusion: sanitation is good, but is better in conjunction with spraying.

Root Transmission

Neely: There is now little doubt that transmission of *C. ulmi* occurs both through insect vectors and grafted roots. Verrall and Graham in 1935 proved root-graft transmission in elms. When using sodium arsenite as a sanitation tool in Batavia, Illinois, we found that "backflash" occurred and that untreated elms were injured due to movement of the silvicide from treated to untreated trees through grafted roots. Using this as a method of graft determination, we found that in Batavia 43 percent of the elms closer than 5 metres were grafted and 29 percent of the elms closer than 3 metres were grafted.

Gene Himelick and I attempted to determine the importance of root-graft transmission in 6 Illinois cities that were utilizing comprehensive disease-control procedures. Of the 199 adjacent tree infections, 22 percent became infected the same growing season, 72 percent became

infected after 1 year, and 6 percent became infected after 2 years. No adjacent tree infections were recorded near trees that had been dead for more than 2 years. Almost all elms within 7 metres of diseased elms were infected within 2 years. Root-graft transmission decreased as distance increased from 7 to 12 metres. Incidence of root-graft transmission in trees at distances greater than 12 metres could not be established.

The soil sterilant SMDC had been reported effective in preventing root-graft infections in the oak wilt disease. We determined that a 7.75-percent concentrate diluted with water 1 to 3 injected into soil was effective in killing elm roots. SMDC poured into 40-cm deep holes, 2 cm in diameter and 15 cm apart, killed all elm roots to a depth of 70 cm. Feeder roots of elm are rarely found below this depth in Illinois.

The efficacy of this method of killing elm roots to prevent root-graft transmission of *C. ulmi* was determined in six municipalities. In the untreated areas, 50 percent of the trees within 12 metres of infected trees became diseased and 86 percent within 7 metres became diseased. In the treated areas, only 19 percent within 12 metres and 29 percent within 7 metres became diseased. The single barrier was effective in 2 out of 3 instances. Later an additional barrier on the far side of the adjacent healthy tree was found almost wholly effective in protecting the second healthy tree. As the SMDC ratio to water was reduced from 1:3 to 1:10, elm root mortality decreased. When the line of injection was within 2 metres of healthy trees, phytotoxicity symptoms were occasionally evident on branches.

Burdekin: The English elm (*Ulmus procera*) produces no visible seeds, and reproduction is by root suckering and coppice growth from felled stumps. Many hedgerows in England often have a common root system extending over several trees.

In experiments of root-graft transmission, the average rate of spread was 2 trees in 2 months from an initial source. The highest rate was 5 trees in 2 months.

There were 600,000 diseased trees in 1971, 1.2 million in 1972, and 2.1 million in 1973. Root transmission undoubtedly contributes much to these figures.

	Infected trees			
Smalley:	*Trees under* observation*	*Root graft***	*Carry-over*	*New infection*
1971 (Milwaukee)	61	0	2	10
1972 (North of Milwaukee	619	24	0	6
1972 (Milwaukee)	696	20	2	19
1973	1627	10	7	23

* Trees not sprayed nor treated, 20-25 years old.
** Trees adjacent to infected trees or to stumps recently removed.

Epstein: Present studies include use of SMDC on excavated roots:

a. SMDC does an incomplete job of killing roots, especially with larger roots.

b. There is often a core of living tissue remaining after SMDC treatment. It is possible that *C. ulmi* can go through the live core; this may explain the 70-percent success claimed by other workers.
c. It takes 15 to 18 days for vacuum applied to the cut end to be interrupted through roots treated with SMDC.
d. *Trichoderma* sp. has been isolated within 3 to 4 days of treatment, and it is highly antagonistic to *C. ulmi*.
e. Non-sporing *Fusarium* sp., which is highly competitive if not antagonistic to *C. ulmi*, has been isolated.
f. So far *Trichoderma* has been isolated from all samples, and the frequency of isolation of *Trichoderma* suggests extensive colonization of the root material.
g. With hot water treatment, there is a rapid formation of tyloses that form an effective barrier in 6 to 7 days.

Smalley: Original tests with SMDC showed no phytotoxicity. However, as used more, toxicity rose; perhaps the chemical company changed the formulation of product. Fresh SMDC is a pretty clear blue; however, as it aged, a black precipitate formed, and this may be the cause of phytotoxicity.

Ryker: What is the position on use of TCPA?

Smalley: TCPA has about the same control as the first treatment with SMDC.

Smalley: Losses from root transmission:
Whitefish Bay (no root-graft control)—losing 30 percent of adjacent elms. Shorewood (with root-graft control measure)— losing 13 percent of adjacent elms.

Sanitation/Control Programs

Smalley: Pruning and tree removal are of utmost importance, but it is difficult to persuade the public. There is very little money in Wisconsin which is appropriated to teach the public control measures for DED. Perhaps we also need a forest or agricultural economist to study the economic aspects of DED.

Burdekin: Considerable efforts were made in the UK to mount a sanitation program, but by the time the organization was set up, there were 1.5 million trees to be removed. Sanitation measures came to a halt because there were insufficient resources to carry out the campaign. Legislation which empowered local authorities to fell diseased trees was therefore rescinded.

Whilst accepting that the basis of DED control should be sanitation, it was felt in these circumstances that Benlate injection techniques might play a small role in helping to preserve valuable elms in high-risk areas. It was therefore decided to start training courses showing the reliable equipment and the use of benomyl dissoved in lactic acid. A concerted effort was made to get man-to-man contact between the researcher and the person using the techniques in addition to informing the public via the news media.

Forest service surveyors conducted the DED surveys and 8 to 10 sur-

veyors were selected to conduct the training courses. They were given the course by Burdekin and Gibbs in exactly the way they were to give it to the course members. Lecture notes were prepared as handouts, illustrated by transparencies. The courses were made available to interested groups and municipalities. Half a day was spent in a classroom, and the other half was spent outside learning about the more practical aspects.

Thomas: In Canada many communities started control measures when DED first appeared, but many gave up when the epidemic began rampaging. However, Sault Ste. Marie, Ottawa, and Fredericton still maintain a good control program including tree removal, spraying with methoxychlor (from helicopter and from the ground), and some root injections in cooperation with the Research Centre.

Stilwell: Fredericton, New Brunswick, is a good example. Since 1957 records were kept of all trees greater than 5 inches dbh, which were removed from the city. Out of 8,000 trees, 1,500 have since been removed, but mainly for street-widening projects. The city has maintained a DED loss rate of less than 1 percent per year. Pruning and tree removal were accomplished promptly whenever possible. Neighboring communities, however, have up to 80 percent dead and dying elm trees, but until this year have not had a serious impact on DED incidence in the city of Fredericton. The disease rate here doubled this year.

GENERAL CONCLUSIONS

It is difficult to draw general conclusions from a conference in which a range of different specialisms were represented, and where several different approaches to the control of Dutch elm disease were discussed. However, there was a remarkable unanimity of view that this problem should be tackled with vigor by pathologists, entomologists, and breeders, together with mycologists, geneticists, and members of other specialist disciplines.

Despite the fact that considerable damage had been inflicted by the disease in both the European and American continents, it was clear that efforts to develop more successful methods of control should be maintained. Promising new avenues have recently been found and it is apparent that each might make its contribution to the control of this disease in the future. However, no single approach is likely to succeed on its own.

The conference agreed that sanitation should be the basis of any control program. A reduction in the population of potential insect vectors breeding in dead or moribund elms is an essential first step. This is particularly important when the disease first moves into a healthy elm population, but also plays an important part when control measures are being carried out in areas where the disease is already present.

New techniques are being developed by the pathologist, involving the use of fungicides that are introduced into the vascular system of the tree, and by the entomologist, involving the manipulation of the life cycle by the use of pheromones or other attractants. The elm breeder, in collaboration with the fungal geneticist, is making an important contribution to the solution of this problem both in the short as well as the long term.

None of these techniques alone is likely to be successful, and it is vital that a combined approach is adopted. Close cooperation between scientists is important, and this confer-

ence may have provided an opportunity for the development of an interdisciplinary approach to the control of this difficult problem.

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